PROCEEDINGS
OF THE
NATIONAL ACADEMY OF SCIENCES

Volume 22 November 15, 1936 Number 11

EFFECTS OF RED SHIFTS ON THE DISTRIBUTION OF NEBULAE

By Edwin Hubble

Mount Wilson Observatory, Carnegie Institution of Washington

Communicated September 24, 1936

Three published surveys with large reflectors and two additional, unpublished surveys furnish homogeneous counts of nebulae to five different limiting magnitudes. The results of Mayall's study of the 36-inch Crossley plates at Mount Hamilton,[1] to $m = 19.0$, have been adopted as published, except that latitude corrections for galactic obscuration have been applied to the counts in order to make them strictly comparable with the Mount Wilson data. The hour exposures only have been extracted from the Mount Wilson surveys[2] with the 60-inch and the 100-inch reflectors, and these counts to $m = 19.4$ and 20.0, respectively, have been reduced separately.

The new surveys, using Eastman 40 plates, represent 20-minute exposures with the 60-inch, $m = 18.47$, and 2-hour exposures with the 100-inch, $m = 21.03$. The counts were reduced to standard conditions by the same methods as were employed in the earlier surveys. Since the new data represent extreme cases, special attention was devoted to the determination of limiting magnitudes, and the quantities are given to another decimal place.

Each survey is confined to the polar caps, $\beta \geqq 40°$, and furnishes N, the number of nebulae per square degree on uniform exposures of excellent quality at the zenith and reduced to the galactic poles. The limiting magnitude, m, represents the threshold of identification which is about 0.5 or 0.6 mag. above the threshold of registration. Comparisons of plates of the same fields made with different exposures confirm the completeness of the counts to the limit m in three of the surveys, and completeness is assumed for Mayall's counts and those on the 2-hour exposures with the 100-inch.

The results are summarized in table 1. Since the frequency distribution of $\log N$ in each survey approximates a normal error-curve, $\log \overline{N}$, the sig-

nificant quantity for the comparison of surveys, is given by the relation

$$\log \overline{N} = \overline{\log N} + 1.151\sigma^2,$$

where σ is the dispersion about $\overline{\log N}$. Direct calculations of $\overline{N}$ give closely similar values, and the means of the two sets of $\log \overline{N}$ are adopted for the comparison.

TABLE 1

DATA FROM INDIVIDUAL SURVEYS*

TEL.	E	NO.	$\overline{N}_1$	m	$\overline{\log N}$	σ	$\log \overline{N}$	$\log \overline{N}$ (OBS.)
60 in.	20	121	19	18.47	1.829	0.224	1.887	1.885
36	60	284	35	19.0	2.103	0.225	2.161	
60	60	214	41	19.4	2.312	0.156	2.340	2.342
100	60	228	52	20.0	2.650	0.176	2.686	2.685
100	120	41	200	21.03	3.154	0.084	3.162	3.162

* Tel. = telescope; E = exposure time in minutes; No. = number of plates; $\overline{N}_1$ = average number of nebulae actually identified per plate; m = limiting magnitude of survey; $\overline{\log N}$ = mean logarithm of number of nebulae per square degree; σ = dispersion in $\log N$; $\log \overline{N} = \overline{\log N} + 1.152\sigma^2$; $\log \overline{N}$ (obs.) = logarithm of the mean number of nebulae per square degree (each plate reduced to standard conditions).

The data are exhibited graphically in figure 1, where $\log \overline{N}$, hereafter called $\log N$, is plotted as a function of m (observed relation). If the apparent, large-scale distribution of nebulae were uniform, the counts should conform to the relation $\log N = 0.6\, m + C$. Actually the observed relation deviates systematically from uniformity by amounts which may be expressed as increments to the magnitudes, Δm. On the reasonable assumption that Δm represents reductions of apparent magnitudes (due to red shifts, space-absorption, etc.) and is a linear function of distance, a least-squares solution gives the following results,[3]

$$\log N = 0.6\ (m - \Delta m) - 9.052 \pm 0.005,$$

where

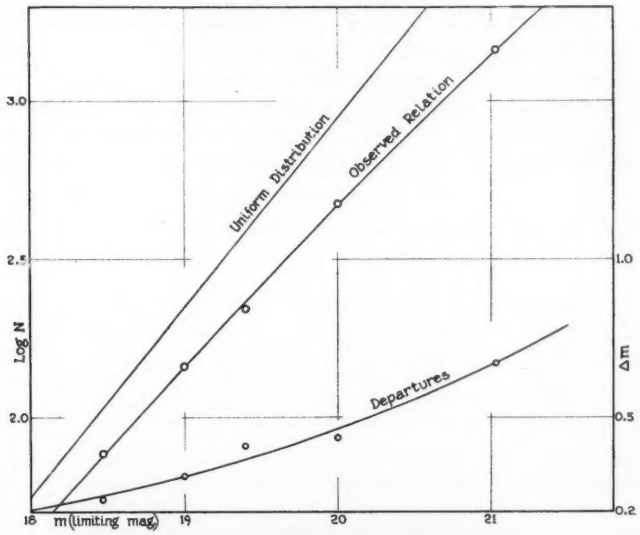
$$\log \Delta m = 0.2\ (m - \Delta m) - 4.239 \pm 0.008.$$

The values of Δm are so small that, in order to avoid a density distribution which increases outward in all directions, space-absorption must be ignored, and the effects referred to red shifts alone.[4] Then, from the velocity-magnitude relation[5]

$$\log v = 0.2\ (m - \Delta m) + 0.77,$$
$$\log d\lambda/\lambda = 0.2\ (m - \Delta m) - 4.707,$$

and

$$\Delta m = 2.94\ d\lambda/\lambda.$$



Apparent Distribution of Nebulae in Depth

The straight line, ***Uniform Distribution***, is the relation log N (per square degree) $= 0.6\ m - 9.052$, which represents uniform distribution with the density equal to that observed in the vicinity of the galactic system. The curve, ***Observed Relation***, is a least-squares solution representing the mean results of the five surveys on the assumption that apparent departures from uniformity, when expressed as corrections to the observed limiting magnitudes, are linear functions of the distance. The solution is $\log N = 0.6\ (m - \Delta m) - 9.052$, where $\log \Delta m = 0.2\ (m - \Delta m) - 4.239$. The curve marked ***Departures*** exhibits the corrections, Δm, as a function of the observed limiting magnitudes, m.

Effects of red shifts may be calculated directly by methods which have been previously discussed.[6] In homogeneous models of the universe which obey the relativistic law of gravitation the effects, depending on whether or not red shifts are velocity shifts, are

$$\Delta m = 5 \log (1 + d\lambda/\lambda) + K \text{ (velocity shifts)},$$
$$\Delta m = 2.5 \log (1 + d\lambda/\lambda) + K \text{ (not velocity shifts)},$$

where K, the reduction of the increments from bolometric to photographic magnitudes, is a function of T_0, the effective temperature of integrated nebular radiation. For $T_0 = 6000°$, which is believed to be of the proper order, the effects are closely approximated, over the range of the surveys, by the linear relations

$$\Delta m = 4d\lambda/\lambda \text{ (velocity shifts)},$$
$$\Delta m = 3d\lambda/\lambda \text{ (not velocity shifts)}.$$

Thus, if red shifts are *not* velocity shifts, the observations lead to a rather simple and thoroughly consistent picture of a universe in which the velocity-distance relation is linear and the large-scale distribution of nebulae is uniform throughout the sample available for inspection. The universe would approximate the Einstein model or a homogeneous expanding model in which spatial curvature and rate of expansion are inappreciable.

TABLE 2

RED SHIFTS NOT VELOCITY SHIFTS

$$\log N - 0.6\,(m_o - 3d\lambda/\lambda) = \text{Constant}$$

m_o	$d\lambda/\lambda$*	$0.6\,(m - 3d\lambda/\lambda)$	log N	CONSTANT CAL.	CONSTANT OBS.	$C-O$
21.03	0.228	12.207	3.162	−9.047	−9.050	+0.003
20	0.158	11.728	2.686	0.042	0.033	−0.009
19.4	0.125	11.414	2.342	0.072	0.077	+0.005
19.0	0.107	11.207	2.161	0.046	0.051	+0.005
18.47	0.086	10.927	1.886	−9.041	−9.044	+0.003

* Calculated from the velocity-magnitude relation, $\log v = 0.2\,(m - \Delta m) + 0.77$, from which $5 \log d\lambda/\lambda + 3d\lambda/\lambda = m_o - 23.535$.

Nevertheless, another fairly consistent interpretation of the observations may be derived on the assumption that red shifts are velocity shifts and measure the rate of expansion of a homogeneous expanding model which obeys the relativistic laws of gravitation. In the first place, the velocity-distance relation must be reformulated. The appropriate data are the mean red shifts and apparent magnitudes of the fifth brightest nebulae in ten clusters distributed over a great range in distance, which have been described in a previous contribution.[7] These data led to a sensibly linear velocity-distance relation when the corrections for red shifts, $\Delta m = 3d\lambda/\lambda$, were applied to the observed magnitudes. If the increments are replaced by $\Delta m = 4d\lambda/\lambda$, the relation evidently departs from linearity by just about the added corrections for recession. A least-squares solution[8] gives $\log d\lambda/\lambda = 0.2064\,(m - \Delta m) - 4.545$.

In accordance with the terminology used in theoretical discussions, the red shift may be expressed as a power series of the distance. Then, to a fair approximation,

$$d\lambda/\lambda = 1.75 \times 10^{-3} r + 2.7 \times 10^{-6} r^2,$$

where the unit of r is a million parsecs. The sign of the second-order term appears to be definitely determined (on the assumption that red shifts are velocity shifts) and the general order of the numerical value cannot be greatly altered without destroying the fit of the observations. The term would indicate that the rate of expansion is diminishing and, consequently, would contract the time interval since the start of the expansion, as calculated from a linear relation.

The corrections to the limiting magnitudes of the surveys, when calculated from the revised velocity-distance relation, indicate a density law which is not uniform but increases systematically with distance. This conclusion, which would assign a unique location to the observer, is unwelcome and *a priori* improbable. However, homogeneity may be restored by postulating sufficient spatial curvature to compensate the residuals introduced by the assumption of recession.

The number of nebulae to the limit m which an observer would record in such a universe is

$$\log N = 0.6\ (m - \Delta m) + F + C,$$

where

$$\Delta m = 4d\lambda/\lambda,$$

and

$$F = \log\left[\frac{3}{2x^3}\left(\sin^{-1}x - x\sqrt{1 - x^2}\right)\right],$$

where $x = r/R_0$ is the distance derived from apparent magnitudes corrected for red shifts,

$$\log r = 0.2(m - \Delta m) + 4.03,$$

expressed as a fraction of R_0, the radius of curvature.[9]

If the term F is expressed as magnitude increments, $F/0.6$, a suitable value of R_0 may be sought, for which the curvature corrections just compensate the residuals, $C - O$, in Δm. Although no precise fit can be found, a value does exist, $R_0 = 1.45 \times 10^8$ parsecs or 4.7×10^8 light-years (log $r/R_0 = -0.11$ for the limit of the deepest survey) which leads to a fairly constant residual, 0.075 mag., that may be considered as a correction to the zero point.

TABLE 3

OBSERVATIONS CORRECTED FOR SPATIAL CURVATURE IN AN EXPANDING UNIVERSE

m_c	$d\lambda/\lambda$	Δm_c*	Δm_o	$D = \Delta m_c - \Delta m_o$	LOG r†	$F/0.6$‡	$D - F/0.6$
21.03	0.231	0.924	0.676	0.248	8.051	0.180	0.068
20	0.158	0.630	0.468	0.162	7.904	0.077	0.085
19.4	0.124	0.500	0.368	0.132	7.810	0.047	0.085
19	0.106	0.423	0.314	0.109	7.746	0.034	0.075
18.47	0.085	0.338	0.253	0.085	7.656	0.022	0.063
					Mean		0.075

* $\Delta m_c = 4d\lambda/\lambda$.

† log r (in parsecs) refers to the observed limiting magnitude of the surveys.

‡ Corrections for curvature are calculated on the assumption that log $r/R_0 = -0.11$ for the limit of the deepest survey ($m_o = 21.03$).

The value of R_0, which is less than the penetrating power of the 100-inch reflector, refers to the present epoch, and corresponds to a mean density for the model of the general order of 10^{-26} gm./cm.^{3} This density

is of the general order of a thousand times less than the local density in the neighborhood of the sun, and a thousand times greater than the smoothed-out density of matter concentrated in nebulae. Since space-absorption appears to be negligible, it is presumably less than 0.1 mag over the light-path to the limit of the deepest survey, 3.5×10^{26} cm. Therefore, a density of 10^{-26} indicates an absorption of less than one magnitude by about 35 grams of matter per sq. cm. cross-section. This condition immediately rules out many forms of matter (for instance, dust, meteoritic material, highly ionized gas) but permits certain other forms (for instance, large chunks and non-ionized gas similar to the earth's atmosphere). The latter are probably not the forms which would be postulated *a priori* for the contents of internebular space, but their existence, with the required density, cannot be ruled out by photometric methods alone.

The assumption that red shifts are velocity shifts thus leads to a particular model of a homogeneous expanding universe.[10] The model is closed and very small—a large fraction can be observed with existing telescopes—and is packed with matter to the very threshold of perception. The rate of expansion has been slowing down so that the past time scale is remarkably limited. In short, the necessary adjustments and compensations suggest that the model may be a forced interpretation of the data.

The assumption that red shifts are not velocity shifts is more economical and less vulnerable, except for the fact that, at the moment, no other satisfactory explanation is known. In the present status of observations and theory, we may evidently choose between a curious, small-scale universe and a new principle of physics.

There is little excuse for the observer to weigh probabilities, because, in due course, the 200-inch reflector will presumably furnish definitive tests. Meanwhile it is possible that theory may develop to the point where the tests are unnecessary or may be made with existing telescopes.

A detailed discussion of the results here summarized is given in a forthcoming *Contribution* of the Mount Wilson Observatory.

[1] *Lick Observatory Bulletins*, **16**, 177 (No. 458) (1934).

[2] *Mt. Wilson Contr.*, No. 485; *Astrophys. Jour.*, **79**, 9 (1934).

[3] The only data which furnish an independent check on the order of the results of the least-squares solution are those in the Harvard survey of bright nebulae (*Harvard Annals*, **88**, No. 2, 1932) for which the corrections, Δm, are negligible. The catalog is believed to be complete to the tabulated magnitude 12.9, which, according to accurate measures with photoelectric cells (Stebbins and Whitford, *Ann. Rept. Mt. Wilson Obs.*, 1935–1936) should be corrected to 12.8. Confining attention to the polar caps and omitting the Virgo cluster with its south-following extension (R. A. 12^h to 13^h, Dec. 0° to +20°; R. A. 12^h5 to 13^h5, Dec. 0° to −15°), we find 592 nebulae to $m = 12.8$, scattered over 14,270 sq. degrees. Hence, $\log N = -1.38$ and $C = -9.06$. Latitude corrections are probably compensated by additional clustering; at any rate, the rather meager data of the survey agree with the least-squares solution from the deeper surveys well within the uncertainties.

[4] If the system of the nebulae were expanding freely in Euclidean space, the observed density should increase outward relative to the true density at the epoch of the surveys. However, an absolute increase would be observed only if the true density now increased outward, or were moderately uniform. The surveys satisfy the latter condition, and the remarkable coincidence suggests the operation of some principle of relativity. This circumstance encourages the selection of relativistic models of the universe for the comparison of observation and theory, although the selection was actually based on other grounds.

[5] *Mt. Wilson Contr.*, No. 549; *Astrophys. Jour.*, **84**, 270 (1936).

[6] The most recent discussion is by Hubble and Tolman (*Mt. Wilson Contr.*, No. 527; *Astrophys. Jour.*, **82**, 302, 1935), where references to earlier papers may be found. Improvements are made by using reflectivities of silver surfaces two to three weeks after burnishing (Strong, *Astrophys. Jour.*, **83**, 414, 1936) rather than of freshly burnished surfaces, and replacing black-body curves by empirical intensity-curves near the limb of the sun, thus reproducing both the line absorption and the observed color excess in nebulae. The results are comparable with those of black-body radiation for $T_0 = 6000°$ with an uncertainty of the order of 200°. The use of solar limb radiation, in order to approximate effects of color excess in the nebulae, follows a suggestion by Baade.

[7] *Mt. Wilson Contr.*, No. 549; *Astrophys. Jour.*, **84**, 270 (1936).

[8] One cluster, Gem. No. 1, was rejected because the latitude correction is very uncertain. The two remaining, outstanding residuals, for Ursa Maj., No. 1 and No. 2, are both of low weight and were combined into a single point. With this procedure, the probable error of the coefficient of $m - \Delta m$ is ± 0.0012. When the fifth brightest nebulae in clusters, $\overline{M} = -16.45$, are replaced by isolated nebulae, $\overline{M} = -15.15$, the constant in the relation is increased by the increment $0.2 \times 1.3 = 0.26$.

[9] The formulae were developed by Tolman (*Relativity, Thermodynamics and Cosmology*, 1934) and were adapted for application to actual observing conditions by Hubble and Tolman, *Mt. Wilson Contr.*, No. 527; *Astrophys. Jour.*, **83**, 302, 1935. The latter contribution includes a preliminary statement of the observational findings which is expanded in the present communication.

[10] The value of R_0, together with the two coefficients in the power series for $d\lambda/\lambda$, determine the cosmological constant, Λ, within the limits $+4.4 \times 10^{-18}$ and $+6.9 \times 10^{-18}$ yrs.$^{-2}$, using Tolman's methods of calculation (*Relativity, Thermodynamics and Cosmology*, p. 472–474). Since Λ is evidently larger than Λ_E (for a possible Einstein universe), the model appears to be that which Tolman designates "as a monotonic universe of the first kind, type M_1," which "expands without reversal from a singular state in the past, . . . at $R_S \geqq 0$, to the final state of an empty de Sitter universe as R approaches infinity" (*loc. cit.*, p. 399).

INDUCEMENT OF FRUIT DEVELOPMENT BY GROWTH-PROMOTING CHEMICALS

BY FELIX G. GUSTAFSON*

DEPARTMENT OF BOTANY, UNIVERSITY OF MICHIGAN

Communicated October 1, 1936

Introduction.—It is a well-known fact that in some interspecific or even in intergeneric crosses of flowering plants the ovary develops into an apparently normal fruit even though no seeds are produced. For years this phenomenon has intrigued the writer. Bearing in mind our present knowledge of growth hormones in plants, it seemed as if the explanation might be that a growth hormone (or hormones) was released into the ovary from the pollen tubes, which usually develop, to some extent, when parthenocarpy occurs. In view of the fact that within the last few years several well-known chemical substances have been found to accelerate growth, cause the root formation in cuttings or otherwise affect growth, it has seemed desirable to determine whether these substances might also induce the ovary to develop into a fruit without pollination.

Methods.—In these experiments indole-3*n*-propionic acid, indole-butyric acid, indole-acetic acid and phenylacetic acid have been used. Of these indole-acetic acid as is well known has been extracted from plants and has been designated as heteroauxin. The first three were used in concentrations of one per cent mixed in hydrous lanolin, while the phenylacetic acid was used in 0.75 and 2.75 per cent also in lanolin.

The plants used were tomato, snapdragon, *Salpiglossus variabilis*, *Petunia hybrida*, *Nicotiana Tabacum* Maryland mammoth variety, *Agapanthus umbellatus*, *Vallota purpurea*, *Zephyranthes carinata* (surprise lily), *Begonia sp.*, Hubbard squash, crook-necked summer squash, cucumber, watermelon, egg plant and pepper. Some of these were grown in the greenhouse during the winter, but others were grown in the field. These plants were chosen either because the flowers were imperfect or the stamens could easily be removed

Usually the flowers of each kind of plant were subjected to three different treatments, and in some instances to four. The flowers were pollinated in the usual way, they were treated with the substance under investigation or they were neither pollinated nor treated with the chemical substance. The last treatment has been designated the control. In some of the early experiments the flowers were also treated with pure lanolin alone, but as there was no effect this treatment was discontinued in later experiments.

Only flower buds that were nearly ready to open and the anthers of which had not yet dehisced were used. The stamens were removed and in the early experiments the lanolin preparation smeared on the stigma. In later

experiments and in all of the experiments with plants grown in the field the style was cut off just above the ovary. This was done to reduce the distance the chemical would have to diffuse to reach the ovary. After the

FIGURE 1

Photograph of a section of a ripe tomato fruit produced by the application of indole-propionic acid to the style of an unpollinated tomato flower. The locules are poorly developed.

stamens had been removed and the style cut, the cut surface was either smeared with the lanolin preparation or left without treatment as a control. In some carefully conducted experiments pollen was placed on the cut sur-

face of the style but there never was any development of the ovary to indicate that fertilization had taken place. It was therefore considered safe and it saved a great deal of time, to leave the treated flowers unprotected by bags. The buds were opened by slitting lengthwise and after the treatment the bud was closed again.

Results with Indole-3n-Propionic Acid.—Tomato, snapdragon, petunia and salpiglossus were treated with this substance.

Tomato: Several dozen flower buds were treated. Lanolin paste containing indole-3*n*-propionic acid was placed both on the stigma, in the early experiments, and on the cut surface of the style, in later experiments. Six externally normal fruits ripened. They ranged in size from 1 cm. to 5.25 cm. The small fruit (only one was produced) was solid tissue with not the slightest trace of locules. The larger fruits developed locules to various degrees (Fig. 1), but in none were the locules and placentae fully developed. No seeds were ever produced, though in one fruit the ovules were of considerable size, but dissection revealed that there was no trace of an embryo, only an ovule shell. In some fruits there was the normal development of a gelatinous mass around the small ovules, but in others the locules were completely empty. No flower bud which was either treated with pure lanolin or left unpollinated or untreated ever showed any increase in the size of the ovary, and after about a week the flower dropped off.

Snapdragon: Numerous flower buds of this plant were used. The ovaries of the flowers treated with indole-propionic acid grew some, but never into full-sized fruits. No seeds were ever observed. There was no observable increase in the ovaries of the control flowers.

Petunia and Salpiglossus: The ovaries of the treated flower buds grew rapidly into fruits of about normal size or even a little larger than normal. These fruits were, however, very much wrinkled, no doubt because of the rapid growth of the ovary wall without accompanying growth of the placentae and seeds, so there was no content to cause the fruits to stretch out and take on a symmetrical shape. No seeds were ever noticed in either of these plants. Growth was at about the same rate as in pollinated flowers. One petunia plant behaved very interestingly, in that when self-pollinated it never produced fruits, yet when treated with indole-propionic acid it produced fruits.

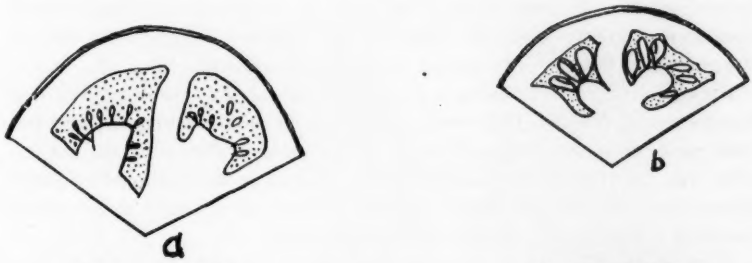
Results with Phenylacetic Acid.—Only tomato, snapdragon and tobacco plants were employed in this experiment and the procedure was the same as in the preceding section, except that in some instances a 0.1 per cent aqueous solution was injected into the ovary through the pedicel. In no instance was there any growth with this latter treatment.

Tomato: Nine externally normal fruits ripened and a number of others commenced growing. These fruits ranged in size from 4.0 cm. to 6.0 cm. in diameter. Both the 0.75 and the 2.75 per cent concentrations were

effective. The internal appearance of these fruits was quite normal except that no seeds were ever produced (Fig. 2).

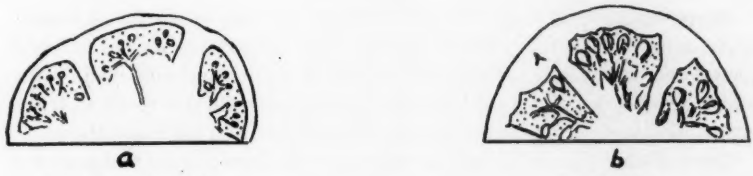
Snapdragon: An examination of a large number of ovaries gave definite evidence that phenylacetic acid had a positive effect upon the growth of snapdragon ovaries. Although the fruits were far from the size of those which resulted from pollination, they showed a marked increase in size over the controls.

Tobacco: Several dozen tobacco flower buds were treated with lanolin paste containing 2.75 per cent phenylacetic acid but in only one instance was there any sign of growth. Usually the flowers dropped off two days



Phenyl acetic acid Normal pollination

FIGURE 2



Indol Butyric Acid Pollinated

FIGURE 3

after they opened unless fertilization took place, but in the instance mentioned the flower remained on the plant for nine days and the ovary was considerably larger than at the time of treatment. The controls always dropped off in two days.

Results with Indole-Acetic Acid.—Tomato, snapdragon, salpiglossus, petunia, begonia, *Zephyranthes carinata*, *Agapanthus umbellatus*, crook-necked summer squash, Hubbard squash, cucumber, egg plant, pepper and watermelon plants were treated with indole-acetic acid. The squashes, peppers, egg plants, watermelons and cucumbers were grown in the field and the others in the greenhouse.

Tomato: Nineteen fruits ripened and many others made some growth.

The ripe fruits ranged in diameter from 3.2 cm. to 5.35 cm. which was somewhat smaller than the fruits produced by pollination on the same plants at the same time. Most of these fruits had poorly developed locules; several having no indications whatsoever of locules. No seeds were produced and usually only a few ovules were present. Controls never developed.

Snapdragon: An examination of treated ovaries gave unmistakable evidence that growth had taken place, yet the ovaries were only about one-third as large as those developed by pollination. They were, however, much larger than the controls.

Salpiglossus and Petunia: The ovaries of both of these plants grew when treated with indole-acetic acid. The resulting fruits were of about normal size but shrivelled. The rate of growth was perhaps a little greater than in the pollinated flowers. There was no growth in the controls.

Begonia: One plant having only pistillate flowers was used. Only three flowers were treated. The ovaries of these increased considerably and became quite green after a few weeks. The treated ovaries were still on the plant two months after treatment. The ovaries of the pollinated flowers did not turn green nor were any seeds developed, though they remained on the plant. Controls dropped off after a few days.

Zephyranthes carinata: Several flower buds were treated. There was considerable growth in the ovary, which did not wither and dry up nearly as soon as the controls.

Agapanthus umbellatus: About twelve flowers were treated with indole-acetic acid. While fruits did not mature, the treated ovaries nevertheless grew to about twice the size of the untreated ovaries and remained on the plants several days longer. The hand pollinations did not result in fruits either, although the plants did produce a few fruits from self-pollinations.

Crook-Necked Squash: Only a few flower buds were treated and since the ovaries of this plant will sometimes grow considerably even in the unfertilized flowers, not enough flower buds were treated to enable one to state positively that growth was induced by the treatment.

Hubbard Squash: Only a few flower buds were treated. There was some growth, usually a doubling of the size of the ovary, but no mature fruits were obtained. The controls did not grow.

Cucumber and Watermelons: Indefinite results were obtained with the few cucumbers and watermelons treated.

Pepper: Fifty flower buds were treated with indole-acetic acid and of these at least six developed into fruits, which though rather small and of slow growth were perfectly normal in external appearance. Sections revealed that the pericarp was of normal thickness, but that there was no development of seeds or placentae. All the forty-eight flower buds left untreated dropped off within a few days.

Egg Plant: These plants were treated late in the summer and at the time of writing, three weeks after treatment, the fruits are still small (about five cm. in diameter) but a fair number of the treated ovaries are developing into fruits. A few that have been sectioned show only lines where the locules would normally be and there are no signs of ovules. The controls are not growing.

FIGURE 4

Photograph of crook-necked summer squashes. (a) Fruit produced by the application of indole-butyric acid to the style of an unpollinated flower. (b) A normal fruit.

Results with Indole-Butyric Acid.—Tomato, snapdragon, *Salpiglossus variabilis*, *Petunia hybrida*, crook-necked squash, Hubbard squash, cucumber, watermelon, peppers and egg plant were employed in the experiments with indole-butyric acid. These experiments were conducted at the same time and usually on the same plants as those with indole-acetic acid.

Tomato: Twenty-one mature fruits were obtained from flowers treated with indole-butyric acid. These fruits were perfectly normal in external appearance. They ranged in size from 2.4 cm. to 6.2 cm. in diameter. The smaller fruits had perfectly solid flesh with no trace of locules. The larger ones usually had, though not always, well-developed locules, but never any seeds. The pericarp was usually somewhat thinner in the fruits produced by the chemical treatment than in those produced by pollination, but the interior was more fleshy (Fig. 3). The artificially produced fruits were in general more fleshy, but they seemed to be more watery. Yet when the moisture content of the fruits was determined it was found to be only 0.3 of one per cent higher than in the fruits produced by pollination.

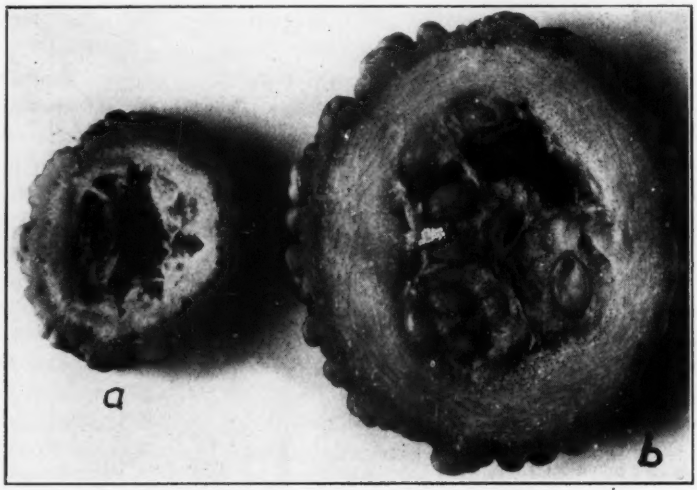


FIGURE 5

Sections of the fruits in Figure 4. Note lack of seeds, a thinner pericarp and lack of the placental development, in fruit (a).

Snapdragons: An examination of a large number of ovaries from flowers that had been treated with indole-butyric acid showed that this substance furthered the development of the fruit. In no instance were these as large as the normally produced fruits but they were always larger than the controls. No seeds were produced.

Salpiglossus and Petunia: Many flower buds of these two plants were treated and the ovaries almost always grew into fruits of normal size but because of lack of content, they were very much wrinkled, and misshapen. The controls never developed. No seeds were ever found in these artificially produced fruits.

Begonia: A few begonia ovaries were treated with indole-butyric acid and like those treated with indole-acetic acid they enlarged and turned green. Eventually they dried up and remained on the plant for over two months, when they were finally removed. The controls did not enlarge any and dropped off in a few days.

Crook-Necked Squash: In this plant it had been discovered that ovaries from unpollinated flowers sometimes grew considerably, and therefore the ovaries from control flower buds as well as treated flower buds were carefully measured. The average of 37 controls gave the following dimensions for the ovary at the time they were dying: length 14.18 cm.; basal diameter 1.98 cm.; greatest apical diameter 1.99 cm. The average dimensions of 39 ovaries from treated flowers were: length 22.64 cm.; basal diameter 3.18 cm.; greatest apical diameter 2.73 cm. The largest individual fruit produced artificially had a length of 44.0 cm., basal diameter 6.4 cm. and apical diameter 5.0 cm. This was approximately as long as a normal fruit and the basal diameter was somewhat greater, but the diameter of the apical end was not quite half that of a normal fruit. Figures 4 and 5 bring out these differences. In the artificially produced fruits the ovary wall was thinner than in normal fruit and the interior, which had no seeds, developed poorly. This accounts for the difference. These data show unquestionably that indole-butyric acid furthered fruit development in the crook-necked summer squash.

Hubbard Squash: Treatment with indole-butyric acid never produced mature fruits, but the ovaries grew to several times their size in the flower buds before they withered, whereas the controls showed only a slight increase if any at all.

Cucumber and Watermelon: Neither of these plants produced mature fruits from flower buds treated with indole-butyric acid, but there was some increase in the size of the ovary beyond that in the controls. So one can say that growth was initiated.

Pepper: From fifty-five flower buds treated with indole-butyric acid, eight externally normal fruits were produced. Sections revealed no seeds and no placental development in these fruits, otherwise they were normal. The forty-eight controls dropped off the plants within a week without any growth.

Egg Plant: As stated under results with indole-acetic acid the egg plants came into blossom late in the summer and at the time of writing there are no large fruits, but many small fruits are developing from the treated flower buds. Sections reveal that there are no seeds developing. Otherwise the parthenocarpic fruits seem normal. Controls have not enlarged.

Discussion and Summary.—These experiments show that certain growth-promoting substances as indole-propionic, indole-acetic, indole-butyric and phenylacetic acids when applied to the cut style often cause the ovary to

grow for some length of time. Mature fruits were not produced in the snapdragon, tobacco, *Agapanthus umbellatus*, *Vallota purpurea*, *Zephyranthes carinata*, begonia, Hubbard squash, crook-necked squash, cucumber and watermelon. Mature fruits without seeds were produced in tomato, petunia, salpiglossus and pepper. At the conclusion of the experiment fruits were developing on egg plants.

The significance of these experiments seems to be that definite chemical substances, which are not specific, cause the ovary of a flower to develop into the fruit. These substances seem to be closely related to the auxins.

* Papers from the Department of Botany and Herbarium of the University of Michigan, No. 609.

THE IMPORTANCE OF ASH ELEMENTS IN THE CULTIVATION OF EXCISED ROOT TIPS

BY WILLIAM J. ROBBINS, VIRGINIA B. WHITE, J. E. MCCLARY AND MARY BARTLEY

DEPARTMENT OF BOTANY, UNIVERSITY OF MISSOURI

Communicated October 13, 1936

Numerous reports have been made of the benefit resulting from the addition of organic supplements or tissue extracts to media in which bacteria,[1] yeasts,[3,11,12] filamentous fungi,[4,9] excised root tips[5,8] or other plant tissues[2] are cultured. It is probable that in some cases the organic supplements are beneficial because of the organic nitrogen supplied or because of something in the nature of an auximone, vitamin, growth hormone or bios. The purpose of the present article is to call attention to the rôle which the ash elements of the organic supplements may play in determining the beneficial effects of such additions to ordinary media.

Robbins[7] reported the limited growth of excised root tips of corn (*Zea mays*) in a modified Pfeffer's solution containing dextrose. Similar results are secured in a simpler and more dilute medium, solution *C*, containing 50 ppm. of calcium nitrate, 10 ppm. of magnesium sulfate, 10 ppm. of potassium dihydrogen phosphate, 1 ppm. ferric chloride and 2% dextrose. The growth of excised corn root tips in this medium prepared with redistilled water, Merck's Reagent chemicals and dextrose of the highest commercial purity is distinctly limited. Grown individually in the dark at room temperature in 150 cc. Erlenmeyer flasks of Pyrex glass in 30 cc. of the above medium the average final length of 225 excised corn root tips originally 1 cm. long in 16 experiments performed at different times was 8.6 cm., with an average of 39 secondary roots per root. The minimum final length of a single root in these experiments was 4.0 cm. with no branch roots and the maximum was 44.1 cm. with 191 secondary roots.

The addition of 0.5% Difco agar to the above medium increases the average growth of the root tips between 5 and 6 times, some of the roots attaining a final length of over 90 cm. with 400 or more secondary roots. The addition of qualitative filter paper (A. H. Thomas #5160 9 cm. circles) has the same effect, a half sheet or one sheet per flask having the maximum effect. Water extracts of agar or of filter paper are similarly beneficial. Quantitative (ashless) filter paper is not effective.

The effect of the qualitative filter paper is illustrated in the following data from an experiment in which excised corn root tips originally 1 cm. long were grown in the dark in 30 cc. quantities of solution *C* for 57 days.

ADDITION TO SOLUTION *C*	NO. ROOTS	AV. FINAL LENGTH CM.	AV. NO. SECONDARY ROOTS	MAX. LENGTH CM.
None	12	8.8	61	12.5
$^1/_2$ sheet filter paper	12	52.6	223	88.3

The benefit conferred by the agar and by the filter paper is due to the ash elements in those substances and not to their physical character or organic content. Untreated ash of the filter paper added in the proportion of 1 mgm. per 30 cc. of medium is as effective as the filter paper itself. Similar results have been secured with agar ash.

We have found also that the agar or filter paper is quite effective if the excised root tips are left in contact with these materials for 24 or 48 hours only. Excised root tips of 1 cm. original length left on 0.5% agar or moist qualitative filter paper for 24 or 48 hours and then transferred to solution *C* grew almost as well as those in solution *C* to which the agar or filter paper had been added. During the 24 or 48 hour period of contact between excised root and agar or filter paper the root apparently accumulates sufficient material from the filter paper or agar to permit almost as much growth as occurs when the agar or filter paper is present in the medium.

Differences in the effect of different brands of dextrose of high purity on the growth of excised corn roots have been observed which may be due to differences in the ash of the samples of dextrose.

The addition of qualitative filter paper to the modified Pfeffer's solution in which White[18] has secured unlimited growth of tomato roots improves that solution also. The tomato roots in White's solution plus filter paper grew more rapidly in our experiments and were whiter and in better condition than in the normal solution.

We are of the opinion that the beneficial effects of the agar ash or filter paper ash is due to these mixtures supplying some elements absent or inadequate in the basic solution and not to their correcting an injurious or toxic condition. We have not determined the effective elements in the filter paper or agar ash. The addition of zinc chloride, manganese chloride and sodium borate at concentrations of 0.1 ppm. is of some benefit but not as much so as the agar or filter paper ash. Copper sulfate (0.001 or 0.01

ppm.) and thallium nitrate (0.005 ppm.) are not beneficial. It is possible that the elements mentioned above were not used at their optimum concentrations but we are inclined to believe that some element or elements other than zinc, manganese, boron, copper and thallium are concerned.

In any event these observations emphasize the necessity of considering the ash elements (even though present in traces only) in interpreting the beneficial effects of organic supplements. They suggest also the usefulness of cultivating excised root tips for the study of the mineral elements essential for the growth of higher plants. The excised root tip is more limited in its supply of stored ash elements than a root attached to a seed or grain from which ash elements are translocated into the attached root and the excised root tips may be expected to show deficiencies more quickly than the plant attached to the seed.

It is of some interest to recall that the original solution used by Pasteur for the cultivation of yeast consisted of

Cane sugar	10 g.
Ammonium tartrate	1 g.
Yeast ash	0.075 g.
Distilled water	100 cc.

Solutions were later devised in which various combinations of salts were substituted for the yeast ash. It seems entirely possible that such solutions are less satisfactory now than when first devised because of the greater purity of the salts secured from manufacturers and readily available for the preparation of the solutions.

We do not mean to imply that a solution composed of mineral salts and dextrose is adequate for the growth of all microörganisms and for the tissues of higher plants including excised roots. We are of the opinion, however, that the mineral salts in many of the basic solutions used in culture work are inadequate in their mineral composition and that the deficiencies are not adequately supplied as contaminants in the mineral salts and carbohydrates of the purity now readily available. When organic supplements to such media are found to be beneficial, it is essential that the rôle of the ash elements in the organic material be determined before conclusions are drawn as to the significance of the organic constituents of such media as has been pointed out by others.[6,10] Details of these investigations will be published elsewhere.

[1] Allison, F. E., and Hoover, S. R., *Jour. Bact.*, **27**, 561 (1934).

[2] Bonner, James, *Proc. Nat. Acad. Sci.*, **22**, 426 (1936).

[3] Hall, H. H., James, L. H., and Stuart, L. S., *Jour. Ind. and Eng. Chem.*, **25**, 1052 (1933).

[4] Leonian, L. H., *Jour. Agr. Res.*, **51**, 277 (1935).

[5] Loo, Tsung-Lē, and Loo, Shih-Wei, *Sci. Repts. Nat. Central Univ. Nanking Sec. B*, **2** 51 (1935).

[6] Richards, O. W., *Jour. Biol. Chem.*, **96**, 405 (1932).
[7] Robbins, W. J., *Bot. Gaz.*, **73**, 376 (1922).
[8] Robbins, W. J., *Bot. Gaz.*, **74**, 59 (1922).
[9] Schopfer, W. H., *Ber. deut. bot. Ges.*, **52**, 308 (1934).
[10] Steinberg, R. A., *Jour. Agr. Res.*, **52**, 439 (1936).
[11] Wildiers, E., *La Cellule*, **18**, 313 (1901).
[12] Williams, R. J., and Saunders, D. H., *Biochem. Jour.*, **28**, 1887 (1934).
[13] White, P. R., *Plant Physiol.*, **9**, 585 (1934).

GROWTH CURVE OF INFANTS

BY C. B. DAVENPORT AND WILLIAM DRAGER

CARNEGIE INSTITUTION OF WASHINGTON, COLD SPRING HARBOR, N. Y.

Read before the Academy, Tuesday, April 28, 1936

When one contemplates the remarkable phenomenon of growth of a child one seeks for an internal factor guiding that growth. One of the simplest explanations of the course of such growth was afforded by Wolfgang Ostwald (1908) and by T. Bradford Robertson (1908, 1923), who found it in a monomolecular autocatalytic reaction. However, as the curve of growth of a child is complex, one has to recognize the probable existence of more than one factor, and Robertson suggests the presence of one factor directing infant growth; and two for later stages. This theory of Robertson is well illustrated by figure 1. If, instead of studying averages, one studies the growth of particular individuals one finds that the course of growth is more complicated, even during infancy, than required by Robertson's hypothesis.

Material and Methods.—This study is based on the growth curves of about twenty babies beginning a few days after birth and measured repeatedly at intervals of two weeks at first, and later of four or more weeks. We have studied them individually to avoid the confusing result of combining many unlike curves. The measurements were made at the Normal Child Development Clinic of Columbia University, located at the Babies Hospital, New York City, under the direction of Dr. Myrtle B. McGraw (Dr. Frederick Tilney, chairman of the Advisory Council).

Results.—We find that the points representing the growth from birth to 2 years cannot be well fitted by a parabola, nor do they lie within any form of a simple logarithmic curve (Fig. 2). The best simple curve that we have found that will pass through the points is an exponential curve on the form $y = 10^{(a + bx + cx^2)}$. The curves corresponding to the points of body weight and height are shown in figures 2, 3 and 4. In the equation the term a in the exponent is the logarithm of size at birth, the second term

of the exponent is a rough measure of the accelerating growth influences, and at age 6 months roughly measures the slope of the growth curve at the period of greatest frowth velocity. The third term may be regarded as roughly measuring the retarding factors in development, which are very marked in the second year (Figs. 2, 3 and 5). A portion of this curve, from 2 to 14 months, is practically a straight line on arithmetic paper. After that age the influence of the x_2 term makes itself felt.

Careful attention to the actual curve of growth as compared with the theoretical, derived from the foregoing formula, indicates that there are in practically all cases two regions of departures from the simple curve. Thus, in the period from five to nine months there is an excess of growth

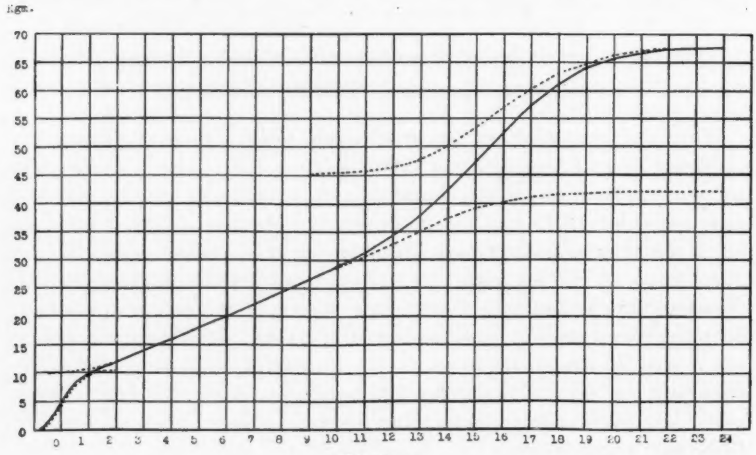


FIGURE 1

The mass curve of human growth in weight to 24 years (continuous line) combined with three hypothetical curves (dotted lines) of monomolecular autocatalytic curves of which it may be considered composed according to the theory of T. B. Robertson. Abscissae, years from conception to 24. Ordinates, kilograms of weight at the given ages. Based on about 100,000 children mostly of Nordic stock.

over the theoretical expectation; and during the period from sixteen to twenty-one months a deficiency (Figs. 2, 3). This appears in practically all children, but in varying degree. Also, the maximum and minimum occur at slightly different times. These facts are brought out more clearly in Fig. 4, in which the simple exponential curve is indicated by a straight line and the lines of growth in stature are indicated as departures from that simple formula.

The correspondence of the different curves is fairly close excepting in the curve of Mahon which is that of a boy who was exceptionally heavy

at birth and who has retained an exceptional chubbiness throughout the first two years of life.

It will be noted too that in a pair of monozygotic twins, as shown in figure 5, the deviation from the theoretical runs somewhat parallel courses in both.

The excess of growth in the middle of the first year after birth amounts to about 5 %; the deficiency in the middle of the second year to about 2.5%. The meaning of these deviations from the simple curve has not as yet been fully worked out. It seems probable that the excess of 6 months is merely due to the influence of the depression at 18 months which

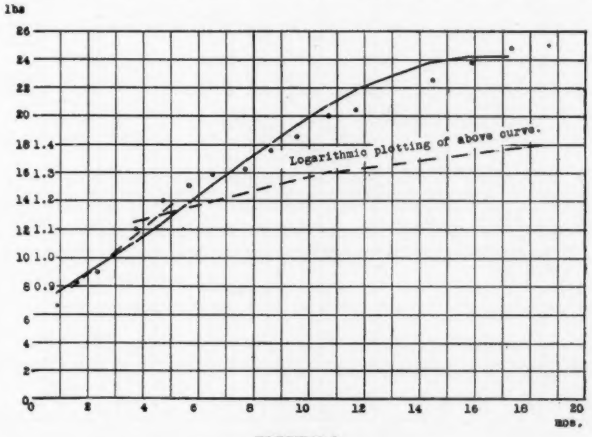


FIGURE 2

Curve of growth of a baby (Carol C.) of Nordic stock from birth (0) to 20 months. The circles represent the actual observed measurements; the continuous curve is computed from all the data using the formula $y = 10^{(a+bx+cx^2)}$. It will be noticed that the continuous curve does not pass through all the small circles. The curve is plotted logarithmically, also; and a striking break appears at $4^1/_2$ months. Upper curve, theoretical curve of C. C: $\log y = 0.8180 + 0.0695x - 0.0021x^2$.

tends to pull down the simple curve at all ages. There is some suggestion that the special exertions of learning to walk and teething may depress the curves both of weight and height at ages 13 to 20 months.

Comparative material is almost non-existent. The nearest approach is that of Bayley and Davis (1935) who measured 61 children repeatedly during three years. They do not publish the individual measurements obtained, but only means for each month to 1 year and less frequently thereafter. We have plotted their findings for the stature of 24 to 30 boys, and passed through these points our curve. The results are shown

in figure 6. Even this curve of averages shows the same tendency to excess of body lengths as observed over the theoretical curve at 6 to 8 months, and of deficiency at 18 to 24 months. These deviations are thus due to no idiosyncrasy of our technique and are probably of general biological significance.

The departures from theoretical do not affect all measurements alike. They are especially clear in total body length and segments of body

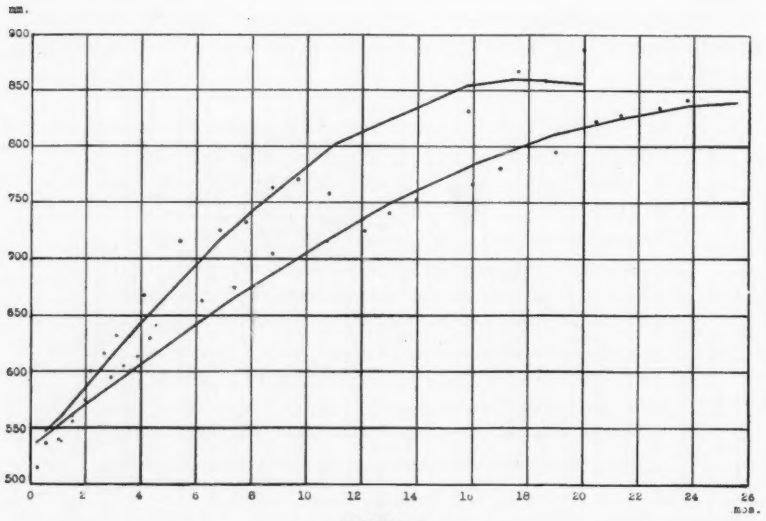


FIGURE 3

Theoretical curves of growth in total body length passing through the points indicated, extending from a few days after birth to 26 months. The points around 6 months lie above the theoretical curve, those at 16 months below. The formulae from which the two curves were drawn are upper curve (J. B. M.) $\log y = 2.7255 + 0.0234x - 0.0007x^2$; lower curve (B. B.) $\log y = 2.7275 + 0.0150x - 0.0003x^2$. The coefficient of the middle term in the right half of the equation is roughly indicative of the slope of the curves at about 6 or 7 months.

length and also in weight. In the case of interspinal pelvic width, however, no such clear phases of departure from the theoretical curve make their appearance (Fig. 7).

Conclusions.—1. The growth curve of the first 24 months of postnatal life is at first rapidly ascending as it is in the latter part of prenatal life. Accelerating factors are effective. As the second year of postnatal life sets in one or more retarding factors make themselves felt and growth slows up. Thus there seems to be a certain justification for the assumption of

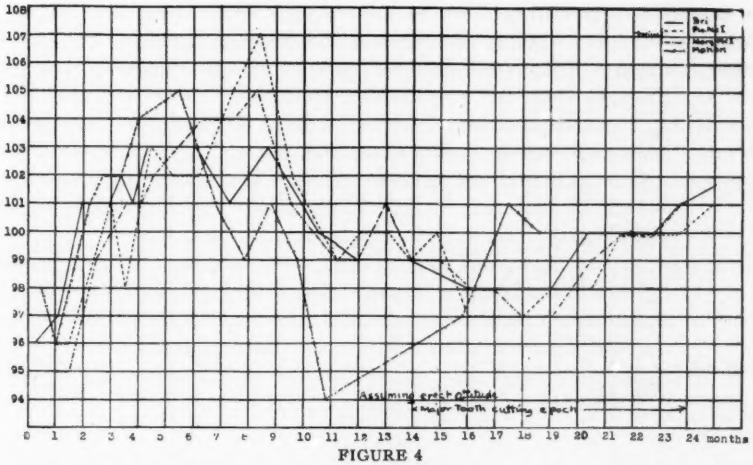


FIGURE 4

A graph to show percentage departures of actual points as measured from a 100% line. This shows the tendency for the statures to be in excess at 6 to 8 months and in deficiency from 16 to 19 months. In the case of one boy, Mahon, characterized by large stature and heavy weight, the departure from expectation is very large and occurs very early, that is about 11 months.

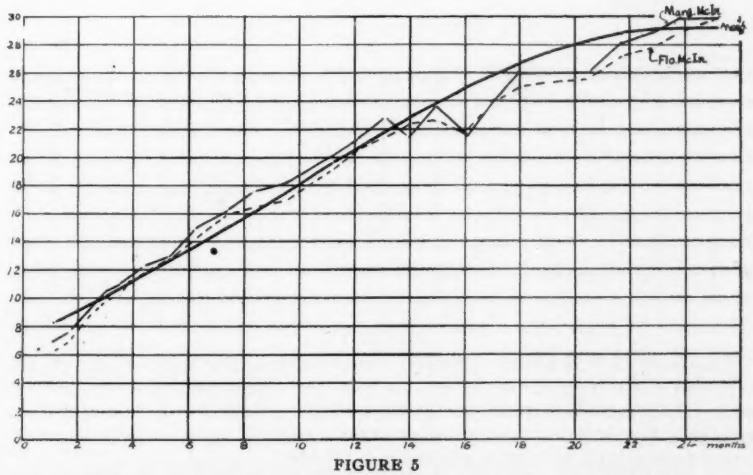


FIGURE 5

Theoretical curve (heavy line) of increase in body weight of one of a pair of monozygotic twins. The actual curves of growth as found are indicated on the chart both for Flo and Marg. The twins depart from the theoretical curve in about the same degree at the corresponding times. Theoretical curve, $\log y = 0.867 + 0.049x - 0.001x^2$.

a monomolecular autocatalytic reaction which fades away at 2 years. Actually there is no fading away but, on the contrary, as figure 2 shows, there is a nearly straight line advance, on the average to about 10 years.

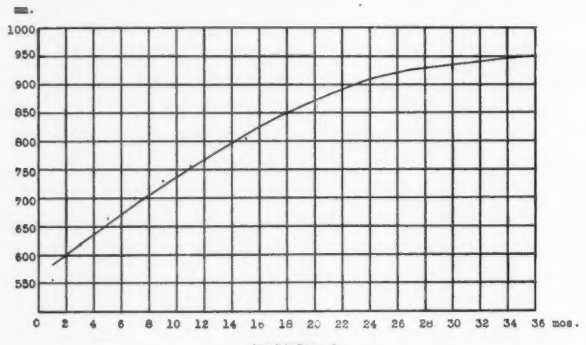


FIGURE 6

Theoretical curve of mass growth in stature (length) of 24 to 31 boys measured repeatedly from first to 36th month, in comparison with averages of actual observations; represented by dots. Data from Table IV of Bayley and Davis, 1935. This shows the resemblance between the departures of the averages from the theoretical curve and those of individual observations from such a curve. Compare with Fig. 2. Theoretical curve, $\log y = 0.7526 + 0.0134x - 0.0002x^2$.

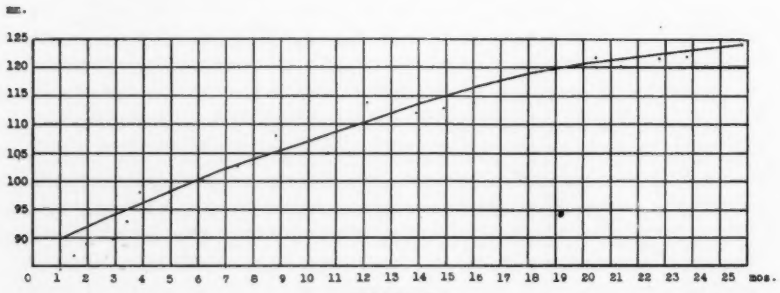


FIGURE 7

Theoretical curve of growth of distance between anterior iliac spines in a girl (B. B.) between 1 and 24 months, together with the individual observations made, indicated by dots. The departures of the observations from the theoretical curve are less regular and apparently less significant than in the case of the height and weight curves. The theoretical curve is $\log y = 1.943 + 0.1063x - 0.000185x^2$.

2. Also the growth curve of the first 12 months is not a simple logistic or S-shaped curve. On the contrary, a period of more rapid growth at

6 to 8 months is followed by a temporary slow growth at 16–18 months, after which growth proceeds at a more rapid pace.

3. Accordingly it is concluded that the growth curve, even in the early months of postnatal life, is not controlled by any single reaction. It is a composite resultant of a lot of more or less independently proceeding growth processes. Indeed, for every period of developmental life the resulting growth curve is probably too complex to be completely expressed in any single formula.

Bayley, Nancy, and Davis, F. C., "Growth Changes in Bodily Size and Proportions during the First Three Years: A Developmental Study of Sixty-one Children by Repeated Measurements," *Biometrika*, **27**, 26–87 (1935).

Ostwald, W., "Über die zeitlichen Eigenschaften der Entwicklungsvorgänge. Vorträge und Aufsätze über Entwicklungsmechanik der Organismen," Hft. V (1908).

Robertson, T. B., "On the Normal Rate of Growth of an Individual and Its Biochemical Significance," *Arch. Entw.-Mech. Organismen*, **25**, 581–614 (1908).

Robertson, T. B., "Chemical Basis of Growth and Senescence," Philadelphia (1923).

MUTATION RATE IN SOMATIC CELLS OF MAIZE

BY DONALD F. JONES

CONNECTICUT AGRICULTURAL EXPERIMENT STATION, NEW HAVEN, CONNECTICUT

Communicated September 25, 1936

Color and other changes in growing plants that may be propagated by vegetative means have long been known. These are often referred to as sports or bud mutations. Many of these variations are now known to be some form of somatic segregation involving a loss or shift of dominant genes rather than any change in a gene itself.

The most frequent color changes in developing maize aleurone result from the removal of one or more dominant genes from one cell and the subsequent multiplication of this deficient cell, allowing recessive genes to come into visible expression. The result may be either a loss or an acquisition of color depending upon the genetic composition of the seeds. Usually the tissues must be in the heterozygous condition with the dominant alleles present singly.

Changes of this kind may also be due to mutation. The evidence from linked genes removed together, from paired mosaics involving a shift of genes, and the evidence from growth alterations accompanying color changes in many cases, all together proves that somatic segregation is by far the more common occurrence. Where the change involves the expression of dominant genes in homozygous recessive material or the alteration

of one of a series of alleles to another in the same series not present in either parent, something other than somatic segregation is indicated.

Six colored spots have been found on otherwise colorless seeds that were originally homozygous *A c R Pr* in composition. These colored spots are made up of individual aleurone cells of the same size and outline as normally colored cells and have the same bluish black color characteristic of dry seeds of *A C R Pr* composition. There is variation in amount of color among individual cells and the spots as a whole are somewhat lighter than most seeds having one dose of *C*. The number of cells in these colored areas varies from 6 to 42. A camera lucida drawing of one of these pigmented cell groups is shown in the accompanying illustration. The number of seeds examined and their composition are shown in table 1.

TABLE 1

COLOR CHANGES IN ALEURONE CELLS OF MAIZE

PEDIGREE NUMBER	GENETIC COMPOSITION	NUMBER OF SEEDS	NUMBER OF SEEDS WITH COLORED CELLS	POSSIBLE CHANGE IN GENES
563 × 142	*a c r pr* × *A C^{I}R Pr*	1866	0	
849 × 142	*A c R Pr* × *A C^{I}R Pr*	371	0	
	Total	2237	0	*C^I* to *C*
849	*A c R Pr*	954	0	
849 × 904	*A c R Pr* × *A c R Pr*	2658	1	
849 × 701	*A c R Pr* × *A c R Pr*	1144	0	
701	*A c R Pr*	1183	5	
701 × 904	*A c R Pr* × *A c R Pr*	2511	0	
	Total	8450	6	*c* to *Ċ*
563 × 85	*a c r pr* × *A C r Pr*	3043	0	*r* to *R*

Seeds homozygous for any one of the recessive complementary genes *a*, *c* or *r* are colorless. In this material dominant *A* and *R* are present and the only way the usual aleurone color can appear is to have dominant *C* present also. All of these stocks have been grown for many years and tested for their aleurone composition. The only way that dominant *C* could be present and not show is to be covered by the inhibitor *C^I*. In heterozygous *C C C^I* seeds faintly colored aleurone cells are visible under the microscope and numerous colored spots result from the loss of the inhibitor. No faintly colored cells of this type are seen in the seeds showing the colored areas and the pigmented cell groups themselves are so rare as to give no support to this possibility.

In the first two families in table 1 recessive *c* is paired with the dominant inhibitor *C^I*. The cells were completely colorless. It was thought that a change from colorless to colored cells might result from the mutation of *C^I* to *C*. This is on the assumption that the inhibitor *I* and the color genes

C and *c* are allelic. The change would be from a dominant to an intermediate position in an allelic series. No indication of such mutations was found. Also no color changes were found in seeds homozygous for *r*.

The six color changes found are most likely the result of a mutation from *c* to *C*. The brown aleurone gene is known to produce color independently of the *A C R* combination but the pigmentation does not correspond to that of the colored spots. There may be other loci that can change in somatic tissue to produce color, that have never been discovered as germinal variations. The change could not be due to somatic segregation uncovering an unknown recessive gene because all but one of the colored areas were found in plants inbred by sib matings. If they were heterozygous for a recessive color gene this color would show by germinal segregation.

FIGURE 1

A camera lucida drawing of a group of colored aleurone cells occurring in an otherwise colorless seed of maize (× 160).

There is the possibility that some external influence can produce color. The aleurone is a single layer of cells surrounding the surface of the seed just below the maternal pericarp tissue. This pericarp is normally transparent. Any injury or infection is easily seen as a break or discoloration in this tissue. Since the seeds are otherwise uncolored and the pericarp above and surrounding the colored areas is intact and clear there is no indication that an outside influence is responsible.

Whatever the change is it seems to be a mutation of some kind. It affects a group of cells all of which have grown from one cell. On colorless seeds single colored cells stand out clearly with a magnification of 30 times under a good light and can be distinguished from small discolorations on the outside surface of the seed. In a rapid examination of a large number of seeds under a lower magnification single cells may be overlooked. For this reason an arbitrary number of at least four colored cells in a group has been taken as the lowest number that can be surely seen. A six-celled group was the smallest number actually found. On a medium-sized seed such as the material examined there are 100,000 or more aleurone cells. This number has been calculated from small areas drawn with a camera lucida. The basal half of the seed is obscured by a thicker and more opaque pericarp and color does not usually appear in the

area overlying the embryo so that only about half of the aleurone cells are clearly visible. Therefore a mutation could occur in any one of 10,000 or more cells in one seed at any stage before the last two divisions and be clearly visible as a group of four or more colored cells against a white background.

If the number of seeds examined is multiplied by this factor a crude mutation rate is arrived at that may be compared with the mutation rate in germ cells and the rate of gene loss in somatic cells. Stadler (*Proc. Sixth Inter. Congress Genetics*, **1**, 274–294 (1932)) finds that most deficiencies are seldom transmitted by the pollen. Therefore changes from a dominant to a recessive condition in cross-fertilized seeds, where the alteration affects the entire seed, are presumably due to mutations transmitted in the germ cells from the dominant parent. From an examination of a large number of seeds Stadler arrives at a mutation rate of dominant to recessive varying from 0.1 per cent for the most frequently mutating gene in the most frequently mutating family to 0.0001 per cent for the least frequently mutating gene.

Comparing these results with the changes found in somatic tissue and with the mosaic rate for the *C* gene in the same family we have the following tabulation:

Most frequently mutating gene	1 in 1,000 germ cells
Least frequently mutating gene	1 in 1,000,000 germ cells
Mosaic rate due to loss of *C*	1 in 70,000 somatic cells
Mutation rate, colorless to color	1 in 14,000,000 somatic cells

The change, colorless to color, is presumably from recessive to dominant and may be expected to occur at a less frequent rate than the reverse change. Stadler's results are measured in number of germ cells and give no clue as to where or when the change takes place. The earlier the mutation occurs in the cell lineage leading to germ cell formation the more frequently will they appear. Possibly most germinal mutations occur in diploid cells and produce visible changes only after recombination takes place. The evidence presented here shows that similar changes also occur in tissues that are not concerned directly with reproduction. While somatic mutations occur with sufficient frequency to be an important factor in aberrant development, considering the large number of cells that may change, they are far less frequent (1 to 200) than the changes due to somatic segregation.

A CYTOGENETIC DEMONSTRATION OF CROSSING-OVER BETWEEN X- AND Y-CHROMOSOMES IN THE MALE OF DROSOPHILA MELANOGASTER

BY CURT STERN AND DOROTHY DOAN

DEPARTMENT OF ZOÖLOGY, UNIVERSITY OF ROCHESTER

Communicated September 25, 1936

It has been suggested[1] that the "attachments" and "reorganizations" involving the *X*- and *Y*-chromosomes in the male of *Drosophila melanogaster*[2] are due to crossing-over. This interpretation became strengthened through Kaufmann's discovery of interchanges between *X*- and *Y*-chromosomes as the cause of the "detachments" of attached *X*-chromosomes in $\widehat{XX}Y$ females.[3] Miss Philip added genetic data indicating double crossing-over in the male between the heterochromosomes.[4] No combined genetic and cytological data had been presented. Such work will be reported below. During the preparation of the manuscript a preliminary note containing similar evidence was published by Neuhaus.[5]

We have found cases of "detachment" in males similar to those investigated in females by Kaufmann. The "detachments" represented a separation of an *X*-chromosome and a small duplication, called Theta (θ), which originally were joined together at the fibre point.[6] It was possible that the detachment process consisted simply of a breaking-apart of the *X*- and θ-chromosomes. On the other hand, it seemed probable that the separation had resulted from crossing-over in the male between the $\widehat{X\theta}$-group and the *Y*-chromosome. In the latter case the detached *X*- and θ-chromosomes should possess complementary parts of the *Y*-chromosome attached to them. The purpose of this investigation was to decide between the above alternatives.

Methods.—In order to obtain detachments of the $\widehat{X\theta}$-group, males of the constitution $\widehat{X\theta}Y$ were mated to females with attached *X*-chromosomes. The *X*-chromosomes of the female were homozygous for yellow while that of the males contained yellow and singed-3. The θ-fragment possesses the normal allele of yellow plus some adjacent loci and the locus of bobbed with a part of the inert region of the *X*-chromosome. The $\widehat{X\theta}Y$ males accordingly were phenotypically not-yellow and singed. If crossing-over occurs in these males four different possibilities have to be considered (Fig. 1): (1) crossing-over between the *X*-chromosome and (*a*) either the long arm of the *Y*-chromosome ("Y^L") or (*b*) the short arm of the *Y*-chromosome ("Y^S"); (2) crossing-over between the θ-part and (*a*) either Y^L or (*b*) Y^S. The cross-over products from these processes are the

chromosome groups $\widehat{XY^S}$, $\widehat{\theta Y^L}$, $\widehat{XY^L}$ and $\widehat{\theta Y^S}$. In the mating described F_1-males carrying "detachments" would contain an $\widehat{XY^S}$ or $\widehat{XY^L}$ group and would be yellow and singed in contrast to the majority of males which are non-yellow singed. F_1-females carrying detachments would contain a $\widehat{\theta Y^L}$ or $\widehat{\theta Y^S}$ group and would be non-yellow in contrast to the majority which are yellow.

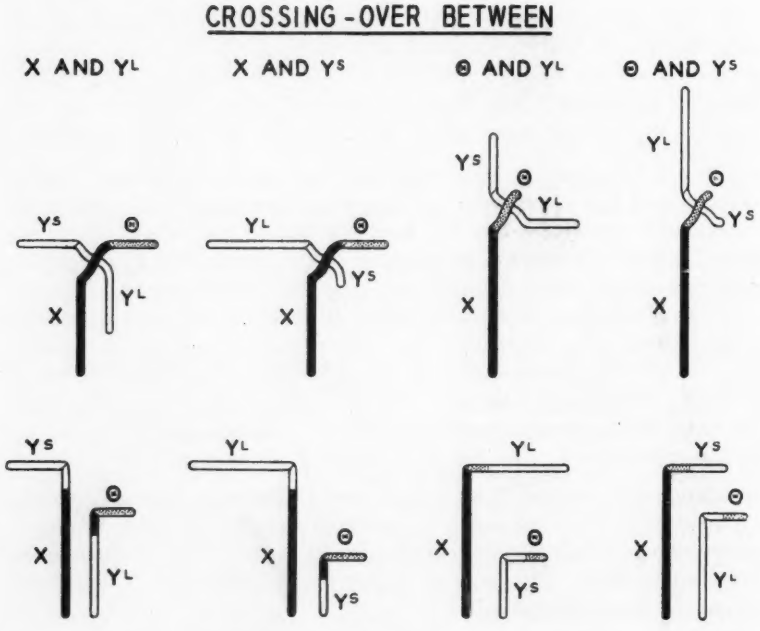


FIGURE 1

Possible modes of crossing-over between the heterochromosomes in $\widehat{X\theta Y}$ males
X-chromosome: black
Y-chromosome: empty
θ-chromosome: dotted

Exceptional F_1-classes are also expected as a result of crossing-over in the *P*-females between the attached *X*-chromosomes and the *Y*-chromosome. While the F_1-males resulting from such a process are readily distinguished by their yellow, not-singed phenotype from those produced in consequence of crossing-over in the *P*-males, the exceptional F_1-females derived from crossing-over in the *P*-females or *P*-males are phenotypically alike. However, they can be separated by progeny tests.

TABLE 1

$\widehat{XXY}$ ♀ × $\widehat{X\theta Y}$ ♂

Experiment	No. of cultures	Total F_1	Detached X	Detached θ
1	20	1636	5	3
2	191	30627	4	5
Total	211	32263	9	8

Results.—Two series of cultures each of which contained 3 *P*-females and, in most cases, 3 *P*-males, yielded 1636 and 30627 F_1-flies (Table 1). Among these there were 17 individuals which resulted from "detachments" in the $\widehat{X\theta Y}$-males. Nine of these were F_1-males and eight F_1-females. Two more females, from experiment (2), may possibly have been of this type but complete sterility made it impossible to determine their origin in respect to detachment in the mother or father.

Of the 8 F_1-females, in 3 cases, from experiment (2), no analysis was possible. When these non-yellow females were mated to unrelated males they produced only yellow daughters and no sons. This result is under-

FIGURE 2

Oögonial figures showing the four different kinds of cross-over products. 2250 ×.

standable under the assumption that the non-yellow females had obtained an attached *X*-chromosome from their mothers and a detached θ-fragment from their fathers and that the $\widehat{XX}$-group during the reduction division segregated to the opposite pole from the θ-fragment. Thus all female offspring would be yellow and all male offspring would carry the θ-piece, besides their *X*-chromosome. As males carrying the θ-duplication are often of very low viability, their absence in the progenies of the three females is not surprising.

There remain 14 cases of detachments of the $\widehat{X\theta}$-group, namely, 9 detached *X*-chromosomes and 5 detached θ-fragments. Stocks containing them were established in order to carry out a genetic and cytological analysis.

The cytological investigation showed in all 14 cases the presence of a chromosome piece attached to the *X*- or θ-chromosome. Two stocks died out before the length of the attached piece had been determined accurately.

In the other 12 stocks it was found to be of a length which corresponded either to that of the long or to that of the short arm of the Y-chromosome. All four possible types of combinations of X- or θ-chromosome with Y^L- or Y^S-attachment were found (Table 2). The cytological determinations were made on the chromosomes of oögonial cells by means of temporary aceto-carmine slides. From all stocks tested at least five completely clear cytological figures were obtained. The diagnosis with respect to a Y^L- or Y^S-arm was made on the basis of length as measured by a comparison with X-chromosomes of the same cell. In the case of the detached θ-chromosomes a normal Y-chromosome in the same cell was also available for comparison.

TABLE 2

CONSTITUTION OF 12 DETACHMENTS OF THE $\widehat{X\theta}$-GROUP

$\widehat{XY^S}$	$\widehat{XY^L}$	$\widehat{\theta Y^S}$	$\widehat{\theta Y^L}$
3	5	3	1

Genetically the nature of the attached Y-chromosome arm was judged by fertility tests. By suitable crosses the $\widehat{XY^{L \text{ or } S}}$ and the $\widehat{\theta Y^{L \text{ or } S}}$ chromosomes were brought together with the Y''-chromosome so that males of the constitution $\widehat{XY^{L \text{ or } S}}\ Y''$ and $X\ \widehat{\theta Y^{L \text{ or } S}}\ Y''$ resulted. (Y'' is a Y-chromosome fragment which has to be supplemented by a Y^L-arm in order to make possible male fertility.) By testing the males of the above mentioned constitution in regard to fertility the presence of a Y^L or Y^S arm could be distinguished. Extensive tests of the 12 available detachments demonstrated fertility in 6 cases and sterility in the other 6 cases, pointing to equal numbers of Y^L- and Y^S-arms. In each detachment the results of cytological and genetic determinations were in agreement with each other.

Discussion.—The experiments demonstrate that crossing-over between the X- and Y-chromosomes occurs in the male of *Drosophila melanogaster.* The question might be asked which parts of the $\widehat{X\theta}$-group and the Y-chromosome cross-over with each other. It was seen (Fig. 1), that $\widehat{XY^S}$ and $\widehat{\theta Y^L}$ as well as $\widehat{XY^L}$ and $\widehat{\theta Y^S}$ groups result from crossing-over either of the Y^L-arm with the X- or θ-chromosome or of the Y^S arm with these chromosomes. The same configurations could also be expected from crossing-over of either arm of the Y-chromosome with the θ-duplication or of either arm of the Y-chromosome with the X-chromosome. The results obtained show that at least two of the four possible types of crossing-over occur. On the basis of Neuhaus' findings[7] regarding crossing-over between the X- and Y-chromosomes it is probable that the two processes in males involved mainly or exclusively the Y^S-arm and both the θ- and the X-chromosomes.

It is a striking fact that the cross-over individuals had a strong tendency to occur together in one and the same culture (Table 3). Furthermore, in the two cultures where a complete analysis of more than one cross-over was possible, only complementary cross-over products were obtained. In one case two detached X-chromosomes showed a Y^S- and one detached

TABLE 3

No. of detachments per culture	0	1	2	4	8
No. of cultures	204	4	1	1	1

θ-chromosome a Y^L-attachment, while in the other case four detached X-chromosomes possessed a Y^L- and two detached θ-pieces showed a Y^S-attachment. The different cross-over products in these cultures may conceivably have arisen from independent events in more than one of the three P-males. On the other hand, it is quite probable that they are the result of crossing-over in one individual. If this latter is true, then either the crossing-over process occurred once at a spermatogonial division resulting in spermatocytes containing complementary cross-overs or there existed a tendency for all crossing-over in the spermatocytes of one individual to take place in the same manner. It is difficult to imagine a uniformity of method in different cells such as the second alternative demands. It seems more probable that crossing-over occurred in one way once in a spermatogonial cell.[8]

If crossing-over occurs at a spermatogonial stage, a calculation of the frequencies of crossing-over has to take account of the fact that probably all cross-overs from one P-male are results of one single process. As the frequency of the cross-over gametes depends upon the early or late spermatogonial stage in which crossing-over occurred, no special significance can be attached to calculations based on the total number of cross-over progeny. It is, however, a striking fact that the frequency of cross-overs varied so greatly in the two experiments reported in table 1.

Summary.—1. In males with X-chromosomes to which the duplication Theta (θ) was attached, separations of the X-chromosome and the θ-duplication were found.

2. Genetical and cytological tests on progeny of 14 different flies containing the separations showed that the disjoined pieces always contained an attachment of one arm of the Y-chromosome. The length of the attachment could not be determined in 2 cases. The remaining cases were represented by four "X-chromosome with Y^L-arm," three "X-chromosome with Y^S-arm," one "θ-chromosome with Y^L-arm," three "θ-chromosome with Y^S-arm."

3. At least two of four different cross-over processes occurred.

4. A consideration of the frequencies and kinds of cross-over products

obtained in individual cultures suggests that crossing-over can occur in spermatogonial divisions.

[1] Darlington, C. D., *Jour. Genetics*, **24**, 65–96 (1931).

[2] Stern, C., *Zeit. Abstgsl.*, **51**, 253–353 (1929); Stern, C., and Ogura, S., *Zeit. Abstgsl.*, **58**, 81–121 (1931).

[3] Kaufmann, B. P., *Proc. Nat. Acad. Sci.*, **19**, 830–838 (1933).

[4] Philip, U., *Jour. Genetics*, **31**, 341–352 (1935).

[5] Neuhaus, M. J., *Nature*, **137**, 996 (1936).

[6] The Theta-duplication had been provided kindly by Prof. H. J. Muller.

[7] Neuhaus, M. J., *Zeit. Abstgsl.*, **71**, 265–275 (1936); *Nature*, loc. cit.

[8] Data concerning spermatogonial crossing-over of autosomes have recently been presented by H. Friesen, *Bull. Biol. Med. Exp.* (*U. S. S. R.*), **1**, 262–263 (1936).

NUMBER OF THE ABELIAN GROUPS OF A GIVEN ORDER

By G. A. Miller

Department of Mathematics, University of Illinois

Communicated September 22, 1936

The identity is the only group of order 1 and this may be regarded as an abelian group even if the law of combination of its operators cannot present itself since there is only one operator in it. There is one and only one group of order 2 and there are two groups of order 4. It will be proved in what follows that these are the only three orders for which the number of abelian groups is as large as half the order of these groups. On the contrary, the number of non-abelian groups of a given order may exceed this order. The lowest order for which this is the case is 32. In fact, 44 of the 51 groups of this order are known to be non-abelian. An Indian mathematician, S. Ramannjan (1887–1920), found an asymptotic formula from which it follows that the number of the abelian groups of order p^{200}, p being a prime number, is nearly four million millions.

Since every abelian group whose order is not a power of some prime number is the direct product of its Sylow subgroups, the number of the abelian groups of order $g = p_1^{\alpha_1} p_2^{\alpha_2}, \ldots, p_\lambda^{\alpha_\lambda}$ ($p_1, p_2, \ldots, p_\lambda$ being distinct prime numbers) is equal to the product of the numbers of the abelian groups of order $p_1^{\alpha_1}, p_2^{\alpha_2}, \ldots, p_\lambda^{\alpha_\lambda}$, respectively. Since the number of the abelian groups of order p^m, p being a prime number, is independent of the value of p, we proceed to prove that the number of the abelian groups of order 2^m, $m > 2$, is less than 2^{m-1}.

To prove this fact it is desirable to bear in mind that the number of the abelian groups of order 2^m is equal to the number of ways in which m

can be separated into positive integral parts so that the sum of these parts is equal to m. When m has been thus separated in every possible manner a partial number of the possible separations of $m + 1$ into such addends can be obtained by adjoining the number 1 to each of the given sets of numbers whose sum is equal to m. It may be assumed that these sets of numbers are so arranged that a number in a set is never followed by a larger number in the same set and that the first n numbers of a given set are separately at least as large as the corresponding numbers of the following set.

To complete the sets of such addends for $m + 1$ we form new sets by replacing the last two numbers of each one of the given sets by their sum whenever this sum does not exceed the third number from the end in this set, and insert the set thus obtained just before the set thus affected. In this manner we obtain at most two sets of addends for $m + 1$ from a given set for m. When $m > 1$ we always obtain two such sets for $m + 1$ from the first set for m but we never obtain more than one set for $m + 1$ from the last set for m. Hence the number of sets of such addends for $m + 1$ is always larger than the number of the sets for m but it is never twice as large, $m > 1$. This proves the theorem that when $m > 2$ the number of the abelian groups of order 2^m is less than 2^{m-1}. Hence there results the following theorem: *The number of the abelian groups of a given order greater than unity cannot exceed a power of 2 whose index is the sum of the largest exponents of the different primes which divide this order diminished by the number of such primes.*

A useful corollary of this theorem is that the number of the abelian groups of a given order greater than unity does not exceed half this order. In fact, it is equal to half this order only when the order is 2 or 4. When all the prime factors of the order of such a group are distinct the given theorem shows correctly that there is only one such abelian group, but when prime factors of the order are repeated a large number of times this theorem will give a number which varies more and more from the number of existing abelian groups as the factors are repeated a larger number of times.

TITANOTHERES FROM THE TITUS CANYON FORMATION, CALIFORNIA

BY CHESTER STOCK

BALCH GRADUATE SCHOOL OF THE GEOLOGICAL SCIENCES, CALIFORNIA INSTITUTE OF TECHNOLOGY

Communicated October 14, 1936

Introduction.—The Titus Canyon formation of Oligocene age, occurring in the Death Valley region of California, was described in a recent paper by Stock and Bode.[1] Brief mention was made at that time of the fossil mammals found in this formation. Among these, the titanotheres were the first to be discovered and moreover are known by the best preserved material. These types possess special interest because of their relationships. They likewise record for the first time the presence of titanotheres in the lower Tertiary of the Great Basin Province. It should be recalled in this connection that titanotheres have been described recently from the Sespe uppermost Eocene of southern California.[2]

Protitanops curryi, n. gen. and n. sp.

Type Specimen.—Skull and jaws, No. 1854, C. I. T. Coll. Vert. Pale., Plate 1, figures 1–3.

Locality.—No. 253, C. I. T. Vert. Pale. Loc., lower red beds of Titus Canyon formation in canyon east of Thimble Peak, Grapevine Mountains, California.

Generic and Specific Characters.—Upper incisors 2; teeth small, crowns oval and non-cingulate. Canines less robust than in *Brontops*. Small diastema between canine and $P\frac{1}{1}$. Premolars with well developed internal cingula, but no external cingula. Nasals long and broad. Horns larger than in *Protitanotherium*, oval in cross-section, but with transverse diameter greater in relation to fore and aft diameter than in Uinta genus. Horns directed outward as well as upward. Dorsal surface of cranium narrow. Size large and intermediate between that of *Protitanotherium emarginatum* and that of *Brontops robustus*. This species is named for H. Donald Curry, discoverer of the first titanothere in the lower Tertiary of the Grapevine Mountains.

Description.—The zygomacephalic index is 71.4 and places *Protitanops curryi* within the brachycephalic division of titanotheres, according to the grouping of skull indices adopted by Osborn.[3] The skull, No. 1854, represents a larger and heavier animal than any so far recorded from Eocene horizons in North America. *Protitanotherium* and *Eotitanotherium* come nearest in size among the late Eocene types. Considerably smaller are the species *Teleodus uintensis* from the Duchesne River horizon and *T. californicus* from the Sespe.

The nasals in specimen No. 1854 are not so long nor so broad as in *Protitanotherium*. They do not taper anteriorly but their antero-internal termination is sharper than in the latter genus. When viewed from the side (Plate 1, figure 1) the naso-maxillary notch is seen to be narrow dorsoventrally and more deeply incised than in typical members of the lower Oligocene group of titanotheres. The lower border of the notch extends well forward, even though the incisor teeth show reduction in number and considerable reduction in size. More is preserved of the left horn than of the right. The dorsal and external surfaces are rugose and the latter shows at least one large abrasion which may indicate that the surface suffered some damage during the life of the individual. Due to some distortion of the skull the left horn extends not only upward but also to the outer side. However, its lateral direction does not appear to be wholly accounted for on this basis and the normal attitude may have involved projection outward as well as upward. When viewed from the top the principal axes of the horns are seen to be slightly divergent toward the anterior end of the skull. This oblique direction of the axis is more markedly displayed in the left horn than in the right.

The zygomatic arches are widely spread and the dorso-external surface of the zygomatic process of the squamosal possesses considerable breadth. On the other hand, the flattened parietal roof of the cranium is quite narrow. In this regard *P. curryi* exhibits apparently a primitive character and certainly differs from the White River types of titanotheres. The lateral cranial surface slopes away from the edge of the dorsal surface in No. 1854, whereas in the later American titanotheres there is definite tendency on the part of the lateral surface to undercut the dorsal plane. The flatness of the parietal plane is continued forward on the frontals and the dorsal profile exhibits no convexity as in the Brontotheriinae. The sides of the frontals above the orbits, as seen from above (Plate 1, figure 2), are parallel.

The post-tympanic process of the squamosal forms a broad plate transversely and encroaches closely upon the surface of the postglenoid process leaving only a narrow space below the external auditory meatus. The occiput is likewise broad transversely and possesses a large and deep median concavity. A small V-shaped notch incises the occipital crest on the middle line.

The upper incisors are small teeth in relation to the size of the skull. Their number is reduced to two on either side of the median line. Unfortunately the lower incisors are not preserved. In size and in presence of smooth oval crowns these teeth emphasize the wide difference between *Protitanops curryi* and the upper Eocene genera of titanotheres and exhibit the progressive characters seen in lower Oligocene forms. The crown of the canine is likewise relatively small and is not swollen. A short space prevails between the canine and the first premolar. No distinct tetartocone

1
2
3

is present in $P\underline{2}$; the deuterocone and tetartocone are represented by a ridge which extends along the inner side of the crown and shows no separation into two cusps. In $P\underline{3}$ the worn surface of the tetartocone is circular in outline and the cusp, while prominent, is still distinctly smaller than the deuterocone. This discrepancy in size between the two cusps is more noticeable in $P\underline{4}$, where the size of the tetartocone is decidedly smaller than that in $P\underline{3}$. Well developed internal cingula are present in the premolars but external cingula are absent. The molars are considerably worn, but show no evidence of the presence of cingula.

The inner border of the upper cheek-tooth series is practically straight and the premolars are not curvilinear as in *Brontotherium*. As seen from the side, however, the series has a curvature with an upward flexure of the premolars.

In the lower jaw the angle extends below the level of the inferior border of the ramus but does not extend very noticeably beyond the level of the condyle. The anterior end of the jaw is not preserved.

Remarks.—Protitanops curryi is certainly more advanced than any of the titanotheres thus far recorded from the American upper Eocene. In comparison to *Protitanotherium* and *Eotitanotherium* the Titus Canyon form possesses better developed horns and considerably more reduced incisors. *P. curryi* is likewise a larger and more advanced form than the titanotheres (*Teleodus uintensis* and *T. californicus*) recorded from the basal Oligocene Duchesne River beds or the uppermost Eocene Sespe. In its large size, brachycephaly, strong zygomata and reduced character of upper incisors, *P. curryi* is more like the lower Oligocene titanotheres of the White River beds. It is, however, distinct from any known White River titanothere in the combination of characters which it possesses, namely, long and broad nasals, narrow and deeply incised naso-maxillary notch, type of horn and narrow dorsal plane of skull.

Resemblance to the brontotheriine titanotheres is shown in the transversely broad occiput, close approach of the posttympanic process to the postglenoid process, wide spread of the zygomatic arches, upward flexure of premolar teeth, presence of tetartocones in posterior premolars and possibly in shape of angle of lower jaw. On the other hand, it differs from *Brontotherium* in the small size of the incisors, absence of cingulate crowns in these teeth, small and non-swollen type of crown in canine, attitude and cross-section of horn and in absence of convexity in profile of the parieto-frontal surface.

PLATE 1

Protitanops curryi, n. gen. and n. sp.

Figures 1, 2, 3. Type specimen, skull, No. 1854, Calif. Inst. Tech. Coll. Vert. Pale. Lateral, dorsal and ventral views; × 1/6. Oblique lines show restored areas.
Titus Canyon Formation, California. Lower Oligocene.

Resemblance to the brontopine titanotheres is indicated in the number, size and type of crown of the incisors, small canine, shape of horn and in the concave profile of the dorsal surface of the skull.

Relationship of the Titus Canyon titanothere is apparently closer to the White River forms than to known upper Eocene types. However, in comparison with the former *Protitanops curryi* is more primitive and suggests in this regard an earlier stage of the Oligocene than that recorded in the White River deposits.

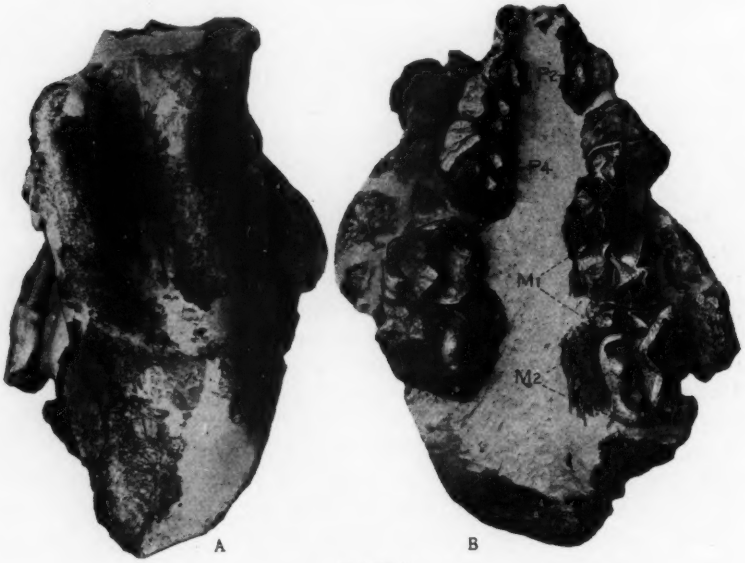


PLATE 2

Menodontine (?) titanothere

Figures A, B. Fragmentary skull, No. 2007, Calif. Inst. Tech. Coll. Vert. Pale. Dorsal and ventral views; approx. × 1/6.

Titus Canyon Formation, California. Lower Oligocene.

MEASUREMENTS (IN MILLIMETERS) OF NO. 1854

Length from tip of nasals to occipital condyles	697
Length from tip of nasals to occipital crest	690
Length from anterior end of premaxillaries to posterior end of condyles	680
Length from anterior end of premaxillary to posterior side of postglenoid process (approximate)	568
Length from anterior end of premaxillaries to postnarial notch	290
Greatest width across zygomatic arches	486
Least width between orbits (approximate)	195
Width of nasals	120

Width of muzzle	82
Least width of parietal roof	82
Greatest width of zygomatic process of squamosal	96
Width across occipital crest	264
Width across condyles	146
Length of horn	103
Width of horn	64
Length from anterior end of canine to posterior end of M^3	330.4
Length of cheek-tooth series of $P\underline{1}$–$M\underline{3}$ (approximate)	272
Distance from top of coronoid process to inferior border of ramus	297
Distance from condyle to inferior border of ramus	277
Depth of ramus at posterior end of $M\underline{3}$	137
Depth of ramus at anterior end of $M\underline{1}$ (approximate)	108

Menodontine? Titanothere.—A poorly preserved facial portion of a skull, No. 2007, C. I. T., Coll. from locality 255, represents a titanothere which is apparently distinct from *Protitanops curryi*. This specimen occurred in the lower red beds of the Titus Canyon formation exposed in the west fork of Titus Canyon, Grapevine Mts., California. Its stratigraphic position is therefore similar to that of *Protitanops curryi*.

This specimen (Plate 2) is smaller than the type of *P. curryi*. At least one molar crown is fairly well preserved. The transverse diameter of the crown, in relation to the anteroposterior diameter, is less in this tooth than in the comparable tooth of *Protitanops*. A faint external cingulum can be discerned on the molars. The premolars ($P\underline{2}$–$P\underline{4}$) are distinctly larger than the comparable teeth in *Protitanops*. As in the latter, the teeth possess strong internal cingula, but they likewise have very faint external cingula. In $P\underline{2}$ a low crest marks the position of the deuterocone and tetartocone. The two inner cusps are distinct in $P\underline{3}$ and $P\underline{4}$. In these teeth the deuterocone is situated well back of the anterior border of the tooth, leaving a distinct shelf in front. The external surfaces of the two outer cusps in $P\underline{2}$ and $P\underline{3}$ are convex and ribbed.

Little is left of the horns, but they appear to possess a round or rudely triangular cross-section.

Relationship of No. 2007 to the menodontine titanotheres among the White River Brontotheriidae is suggested particularly by the elongate molars and to some extent also by the basal cross-section of the horn.

[1] Stock, C., and Bode, F. D., *Proc. Nat. Acad. Sci.*, **21**, 571–579 (1935).
[2] Stock, C., *Proc. Nat. Acad. Sci.*, **21**, 456–462 (1935).
[3] Osborn, H. F., *U. S. Geol. Surv. Mon.* **55**, 1, 259(1930).

ON THE SATURATION OF EXCHANGE FORCES

BY E. WIGNER

DEPARTMENT OF PHYSICS, PRINCETON UNIVERSITY

Communicated October 6, 1936

1. Bethe and Bacher[1] mention in their article on Nuclear Physics that the present author has given a proof for the saturation property of the so-called Majorana[2] and Heisenberg[3] forces. It is intended to give this proof in the following pages, together with the exact conditions for it. The most important of these is that it applies only to interactions depending on the distance like

$$J(r) = -\int_0^\infty g(\rho) f(r/\rho) d\rho, \tag{1}$$

where $g(\rho)$ is a nowhere negative integrable, otherwise arbitrary function

$$f(r) = \begin{matrix} (2\pi/3)(2 - 3r/2 + r^3/8) & \text{for } 0 \leq r \leq 2 \\ 0 & \text{for } r \leq 2. \end{matrix} \tag{2}$$

This is the common part of the volume of two spheres of radius 1 at the distance r. It would appear that a rather general class of functions can be represented in the form (1). For these functions, it will be shown that the expectation value of H_n

$$(\Psi_n, H_n \Psi_n) \tag{3}$$

for any antisymmetric normalized function of n sets of variables has a lower bound which is proportional to n (and not n^2), if

$$H_n = \sum_{i,k=1}^{n}{}' J(r_{ik})(P_{ik} + C). \tag{4}$$

It is usual to omit the values $i = k$ from the summation, P_{ik} means the exchange of the space coördinates $\mathfrak{r}_i$ and $\mathfrak{r}_k$ for Majorana forces; C is 1/4 in this case. It means the exchange of both space and spin coördinates for Heisenberg forces; C is then 1/2, as usual $\mathfrak{r}_{ik} = |\mathfrak{r}_i - \mathfrak{r}_k|$. The wave functions $\Psi(\mathfrak{r}_1\sigma_1\tau_1, \ldots, \mathfrak{r}_n\sigma_n\tau_n)$ contain in addition to these variables the isotopic spin variables τ which also can assume two values: 1 for neutrons, -1 for protons. The antisymmetry means equations of the type

$$\Psi(\mathfrak{r}_1\sigma_1\tau_1\mathfrak{r}_2\sigma_2\tau_2 \ldots.) = -\Psi(\mathfrak{r}_2\sigma_2\tau_2\mathfrak{r}_1\sigma_1\tau_1 \ldots), \text{ etc.} \tag{5}$$

2. We may notice, first of all, that H_n is diagonal in the coördinates and it is sufficient, hence, to consider such functions which are different from zero only for those configurations which arise from the $\mathfrak{r}_1 = \mathfrak{a}_1 \ldots \mathfrak{r}_n = \mathfrak{a}_n$ configuration by an arbitrary interchange of the $\mathfrak{a}$'s. This last must be

allowed in order to satisfy the condition of antisymmetry. What we are interested in can be written hence without an integral: it is the minimum value of

$$\sum_{ik}{}'\Psi(\mathbf{a}_1\sigma_1\tau_1 \ldots \mathbf{a}_i\sigma_i\tau_i \ldots \mathbf{a}_k\sigma_k\tau_k \ldots \mathbf{a}_n\sigma_n\tau_n)^* J(|\mathbf{a}_i - \mathbf{a}_k|) \cdot [\Psi(\ldots \mathbf{a}_k\sigma_i\tau_i \ldots \mathbf{a}_i\sigma_k\tau_k \ldots) + C\Psi(\ldots \mathbf{a}_i\sigma_i\tau_i \ldots \mathbf{a}_k\sigma_k\tau_k \ldots)] \tag{3a}$$

for Majorana forces, and a corresponding expression for Heisenberg forces. Expression (3a) has to be minimized, by properly choosing the $\mathbf{a}_1 \ldots \mathbf{a}_n$ and the function Ψ, which, however, must satisfy (5); then the behavior of the minimum for increasing n must be investigated.

We first consider the expression (4) for the Hamiltonian

$$H_n^0 = -\sum_{ik}{}'(P_{ik} + C). \tag{6}$$

This corresponds to unit interaction within a sphere surrounding all the particles. We can develop Ψ in the following way

$$\Psi(\mathbf{r}_1\sigma_1\tau_1 \ldots \mathbf{r}_n\sigma_n\tau_n) = \sum_{s\kappa} b^s_{\kappa\mu}\psi^s_\kappa(\xi_1 \ldots \xi_n) f^s_{\kappa\mu}(\eta_1 \ldots \eta_n). \tag{7}$$

Here ξ stands for $\mathbf{r}$ in case of Majorana forces, for $\mathbf{r}$ and σ in case of Heisenberg forces; η for σ,τ in the first case, for τ alone in the second case. The $f^s_{\kappa\mu}(\eta_1 \ldots \eta_n)$ is the function which belongs to the κ row of the irreducible representation S of the interchange of η's and to the μ row of the irreducible representation S of the group of rotations in the η space. The result must clearly be independent of μ. The function $f^s_{\kappa\mu}$ is known to be defined up to a factor by these requirements, S may be considered at present as any numeration of the irreducible representations. If (7) is antisymmetric the ψ^s_κ must belong, with respect to the interchange of the ξ, to the κ row of the representation which is adjoint[4] to S. (Adjoint representations have equal matrices for even permutations, and oppositely equal matrices for odd permutations.) The $f^s_{\kappa\mu}$ are supposed to be normalized and we have then[4] $b^s_{1\mu} = b^s_{2\mu} = \ldots b^s_{n\mu} = b^s$.

We have, because of the orthogonality of the f,

$$\begin{aligned}(\Psi, P_{ik}\Psi) &= \sum_{s\kappa} |\, b^s_{\kappa\mu}\,|^2 (\psi^s_\kappa, P_{ik}\psi^s_\kappa) \\ &= \sum_{s\kappa\lambda} |\, b^s_{\kappa\mu}\,|^2 (\psi^s_\kappa, -D^{(s)}(ik)_{\lambda\kappa}\psi^s_\lambda) \\ &= -\sum_{s\kappa} |\, b^s_{\kappa\mu}\,|^2 D^{(s)}(ik)_{\kappa\kappa} = -\sum_S |\, b^s\,|^2 \chi^{(s)}(T).\end{aligned} \tag{8}$$

Here $-D^{(s)}(ik)_{\lambda\kappa}$ is the $\lambda\kappa$ matrix element of the matrix which corresponds to the transposition (ik) in the representation adjoint to S, and $-\chi^{(s)}(T)$ is correspondingly the character. The normalization of Ψ means

$$\sum_s |\, b^s\,|^2 \chi^{(s)}(E) = 1, \tag{9}$$

where E is the unit element. Since all the $(\Psi, P_{ik}\Psi)$ are equal

$$(\Psi_n, H_n^0\Psi_n) = -n(n-1)\sum_s |b^s|^2 (-\chi^{(s)}(T) + C\chi^{(s)}(E)). \quad (10)$$

This will be a minimum satisfying (9) if $|b^s|^2 = \chi^{(s)}(E)^{-1}$ for that S for which $\chi^{(s)}(T)/\chi^{(s)}(E)$ has the smallest value, and all the other b^s are zero.[5] The value of the minimum is

$$(\Psi_n, H_n^0\Psi_n)_{\min} = n(n-1)(\chi^{(s)}(T) - C\chi^{(s)}(E))/\chi^{(s)}(E). \quad (10a)$$

For Heisenberg forces, S must be a representation the partition of which contains not more than two figures; for Majorana forces, not more than four figures. The ratio is smallest[6] in the former case for the partition $n/2 + n/2$, in the latter case $n/4 + n/4 + n/4 + n/4$. For the first case, we have

$$\chi^{(s)}(T) = \frac{(n-2)!(n-4)}{(n/2+1)!(n/2-1)!}\,; \quad \chi^{(s)}(E) = \frac{n!}{(n/2+1)!(n/2)!} \quad (11)$$

in the second case

$$\chi^{(s)}(T) = \frac{(n-2)!4!(n/2-8)}{(n/4+3)!(n/4+2)!(n/4+1)!(n/4-1)!} \quad (11a)$$

$$\chi^{(s)}(E) = \frac{n!3!2!}{(n/4+3)!(n/4+2)!(n/4+1)!(n/4)!}.$$

Inserting the values of $C = 1/2$ in the former, $1/4$ in the latter case, we have

$$(\Psi_n, H_n^0\Psi_n)_{\min} = -c'n \quad (12)$$

with $c' = 3/2$ in the Heisenberg, $c' = 15/4$ in the Majorana case. These are the minima of the potential energy if the interaction has unit strength and the distance of the particles is small compared with the action of the force. The expectation value of H_n^0 can certainly reach the limit (12).

3. We next proceed to the general case in which the distances $|\mathbf{a}_i - \mathbf{a}_k|$ are not small compared with the range of forces. We draw a sphere with radius ρ around an arbitrary point $\mathbf{a}$ and consider then the interaction $(\Psi, (P_{ik} + C)\Psi)$ between all particles within the sphere $|\mathbf{a}_i - \mathbf{a}| < \rho$, $|\mathbf{a}_k - \mathbf{a}| < \rho$ assuming unit interaction for these. The result will be a function of $\mathbf{a}$ which we shall integrate over the whole space and denote the integral by I. We can calculate I in two ways: either first performing the integration, then the summation over i and k, or else the other way around.

If we integrate over the term

$$\Psi(\ldots \mathbf{a}_i\sigma_i\tau_i \ldots \mathbf{a}_k\sigma_k\tau_k \ldots)^*[\Psi(\ldots \mathbf{a}_k\sigma_i\tau_i \ldots \mathbf{a}_i\sigma_k\tau_k) + C\Psi(\ldots \mathbf{a}_i\sigma_i\tau_i \ldots \mathbf{a}_k\sigma_k\tau_k)] \tag{13}$$

it will appear only for that portion Q_{ik} of the space the points of which are nearer than ρ both to $\mathbf{a}_i$ and $\mathbf{a}_k$. Since the volume of Q_{ik} is $\rho^3 f(|\mathbf{a}_i - \mathbf{a}_k|/\rho)$, the term (13) contributes

$$\rho^3 f(|\mathbf{a}_i - \mathbf{a}_k|/\rho)\, \Psi(\ldots \mathbf{a}_i\sigma_i\tau_i \ldots \mathbf{a}_k\sigma_k\tau_k \ldots)^* \cdot [\Psi(\ldots \mathbf{a}_k\sigma_i\tau_i \ldots \mathbf{a}_i\sigma_k\tau_k \ldots) + C\Psi(\ldots \mathbf{a}_i\sigma_i\tau_i \ldots \mathbf{a}_k\sigma_k\tau_k \ldots)] \tag{13a}$$

to I. The whole I is then obtained by summation of (13a) over i and k. This is, however, because of (3a) just the total interaction

$$\mathrm{I} = (\Psi_n, H_n\Psi_n) \tag{14}$$

for $J(r) = \rho^3 f(r/\rho)$.

If we calculate I by first summing over i and k and then integrating, we must first decompose the whole space into $n + 1$ sections V_0, V_1, V_2, ..., V_n. If $\mathbf{a}$ lies in V_s, there are just s points $\mathbf{a}_i$ within the sphere. Clearly, then

$$V_1 + 2V_2 + \ldots + nV_n = n4\pi\rho^3/3, \tag{15}$$

since every point is covered by all spheres the centers of which have a distance smaller than ρ from the point.

If the center of the sphere is in V_s, the integrand of I is the total potential energy of a system of s particles under the interaction (6). The integrand in V_s is, hence, greater than $-c's$. The whole integral I is, consequently

$$\begin{aligned} \mathrm{I} &\geq -c'V_1 - 2c'V_2 - \ldots - nc'V_n \\ \mathrm{I} &\geq -c'n4\pi\rho^3/3. \end{aligned} \tag{16}$$

Because of (14), this means that

$$(\Psi_n, H_n'\Psi_n) \geq -4\pi c'n/3 \tag{17}$$

for

$$H_n' = \sum_{ik}{}' f(|\mathbf{r}_i - \mathbf{r}_k|/\rho)(P_{ik} + C).$$

If H_n is the integral (4) (1) over H_n' with positive weights $g(\rho)$, the expectation value will certainly not be smaller than

$$(\Psi_n, H_n\Psi_n) \geq -4\pi c'n \int_0^\infty g(\rho)d\rho/3, \tag{18}$$

and goes, hence, with the first power of n.

It is clear that if C is replaced by a smaller value, the conclusion holds *a fortiori*. If the forces act only between different kinds of particles, the con-

siderations of section 2 will be affected. One must consider then, separately, the subgroup containing interchanges of like particles and subtract the energy resulting from the interaction of these from (10). It is well known that C must be 0 in this case.

The problem underlying the present discussion has been considered recently by Breit and Feenberg[7] by means of the statistical model. Breit and Feenberg consider more general interactions than our H_n. Since they use the statistical method they obtain only upper limits which their constants g, g_1, g_2 (which correspond to our C) certainly cannot surpass. These upper limits, if specialized to the two cases considered here, just give $C = 1/4$ for Majorana and $C = 1/2$ for Heisenberg forces. The present calculation shows, hence, that their conditions in the two cases considered here give not only necessary but also sufficient conditions for the saturation property. This is not so surprising, perhaps, since section 3 shows that the potential energy will not be lowered by expanding the nucleus in any way and section 2 shows that, for a very small nucleus, it depends only on the transformation property of the wave function. The wave function of the statistical model has, however, the correct behavior in this respect, at least for the term which turned out to be the lowest one.

[1] H. A. Bethe and R. F. Bacher, *Rev. Mod. Phys.*, **8**, 82 (1936).

[2] E. Majorana, *Zeit. Phys.*, **82**, 137 (1933).

[3] W. Heisenberg, *Zeit. Phys.*, **77**, 1 (1932). In these two papers the interaction is assumed to exist only between proton-neutron pairs. The present paper deals here with an equal interaction between all kinds of particles, which is now known to be nearer to actual facts. The calculation is simplified by this newer assumption. For the original assumption of Heisenberg $C = 0$ must be set in (4).

[4] Cf., e.g., E. Wigner, *Gruppentheorie*, etc., Braunschweig 1931. Chapter XXII.

[5] We should have seen, to begin with, that the characteristic functions will belong to a representation of the permutations and rotations of the η, since these do not enter into the Hamiltonian.

[6] The characters of the representations of the symmetric group were determined by G. Frobenius, *Berl. Ber.*, 516 (1900).

[7] G. Breit and E. Feenberg, to appear shortly in *Phys. Rev.*, 50, 1936.

THE TRIPLE INNERVATION OF THE CRAYFISH MUSCLE

BY A. VAN HARREVELD AND C. A. G. WIERSMA

WM. G. KERKHOFF LABORATORIES OF THE BIOLOGICAL SCIENCES, CALIFORNIA INSTITUTE OF TECHNOLOGY

Communicated September 21, 1936

Since the publications of Biedermann (1887) and Hoffmann (1914) on the double innervation of crayfish muscle it has been believed that these muscles are each innervated by two kinds of axons. The stimulation of one kind of these axons would cause a contraction of the muscle; the stimulation of the other kind would inhibit this contraction. However, Wiersma and van Harreveld (1936) showed that the fast and the slow contraction which can be elicited in most of the muscles of the cheliped in *Cambarus clarkii* and *Astacus trowbridgii* are caused by the stimulation of two different axons, and thus no nerve fibre was left for the peripheral inhibition.

Investigating preparations stained with methylene blue we have found that the innervation by two axons is only true for two muscles of the cheliped of *Cambarus clarkii*, namely, for the abductor of the dactylopodite and for the extensor of the propodite. The other muscles of the cheliped are innervated by three nerve fibres which branch each time at the same place (triplotomic branching). In one of these muscles (flexor of the propodite) it could be proved that the stimulation of the thickest of the three fibres causes a fast contraction, the stimulation of the intermediate-sized fibre elicits a slow contraction of the muscle, and the stimulation of the thinnest of the fibres gives inhibition of the contraction caused by the stimulation of either of the two other fibres.

The stimulation of one of the two fibres running to the doubly innervated muscles (abductor of the dactylopodite and extensor of the propodite) causes a contraction, the other elicits an inhibition of this contraction. The axon causing the contraction is common to both muscles, as has been found in preparations stained with methylene blue as well as by stimulating that fibre. Thus these two muscles can be considered as parts of one motor unit. The two muscles receive different inhibiting fibres.

The muscles of the cheliped of a few marine crustaceans were investigated (*Randallia ornata*, *Blepharipoda occidentalis* and *Cancer anthonyi*), and it could be shown that they are all triply innervated, even those muscles which in *Cambarus clarkii* are only doubly innervated.

ON THE NATURE OF AURAL HARMONICS[1]

BY S. S. STEVENS AND E. B. NEWMAN

HARVARD UNIVERSITY, SWARTHMORE COLLEGE

Communicated September 22, 1936

The common observation that stimulation of the ear by purely sinusoidal wave gives rise to the perception of aural (subjective) harmonics is generally ascribed to the non-linear and asymmetrical characteristics of the ear, viewed as an electro-mechanical transducer. Estimates of the magnitudes of aural harmonics have been made by indirect means (Fletcher[2]), and are such as to indicate a high degree of distortion for tones of great intensity.

It can be shown that the motion of a system under an impressed sinusoidal force will not be sinusoidal unless the system obeys Hooke's law, i.e., unless the displacement is proportional to the applied force. In general, the resulting motion in a non-linear system can be described in terms of a Fourier series. However, if the departure of the system from linearity (Hooke's law) is symmetrical in both directions from the position of rest, the Fourier series will contain only odd terms. Thus in the analogous case of electronic vacuum-tubes connected in "push-pull," there is present in the output circuit only the fundamental frequency and its odd harmonics. On the other hand, if the system is not symmetrical on either side of the operating point (position when no force is applied) even as well as odd harmonics will be present in the resulting motion. An analogous case, for example, is found when "push-pull" arrangement is unbalanced.

Now, it is clear that the aural harmonics contain both odd and even components. The problem, then, is to account for them in terms of non-linearity and of asymmetry.

In order to observe the aural harmonics directly, we examined the electrical potential generated in the cochleas of animals. Between a pair of electrodes, one in contact with the round window of the cochlea and the other in contact with the muscles of the neck, one obtains an electrical potential, presumably generated by the hair cells of the organ of Corti (Stevens and Davis[3]), which appears to be directly proportional to the distorting force to which the hair cells are subjected. We amplified these potentials and led them to a cathode-ray oscillograph and to a wave-analyzer (General Radio, type 636A). Then, on stimulating the ear with pure tones of various frequencies and intensities, the behavior of the aural harmonics could be observed under various conditions.

Typical results for a cat, under dial anesthesia, are shown in figure 1. The relative magnitude of the electrical response at the fundamental frequency of 1000 cycles and of each of the harmonics was measured by the

wave-analyzer for various sound intensities. The harmonic content (2nd) of the stimulating tone was less than 0.5%, an amount which means that it was negligible in comparison to the size of the aural harmonic. It will be noted that the second harmonic makes its appearance at about 40 db above threshold and increases rapidly in size, up to the point at which the fundamental approaches its maximum. Then the second harmonic decreases, while the third continues to grow until it finally exceeds the second.

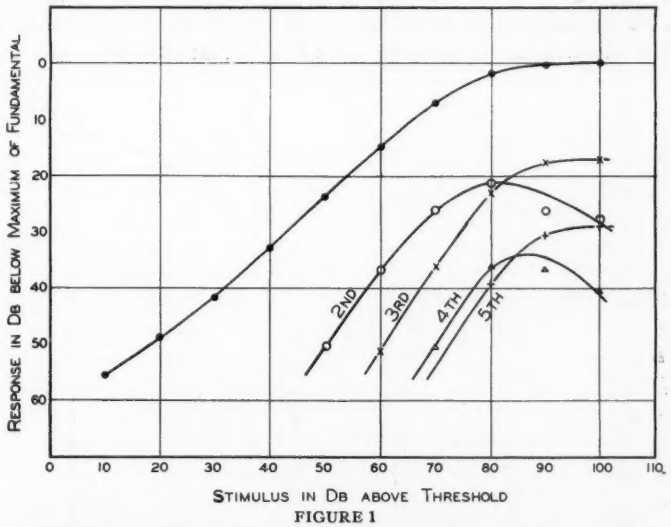


FIGURE 1

Analysis of the cochlear response of a cat when stimulated with a pure tone of 1000 cycles. Abscissa values represent the intensity of the stimulus in decibels above the human threshold. The ordinate scale is in decibels below the maximum value of the fundamental. The uppermost curve shows the magnitude of the fundamental in the response when the ear is stimulated with sound intensities plotted along the abscissa. The other curves in order show the magnitude of the second, third, fourth and fifth harmonics. Thus the intersections along any given vertical line give the relative magnitudes of the first five partials in the response when the ear is stimulated with a given tone.

A similar relation obtains between the fourth and fifth harmonics. In general, the even harmonics pass through a maximum, whereas the odd harmonics appear not to decline.

The same effect is shown in figure 2 for the case of a guinea pig. Nor is this result peculiar to tones of 1000 cycles. All frequencies show the same phenomenon, within our ability to measure them. At low frequencies the relations are complicated by the presence of anomalous effects due to action currents (presumably from the auditory nerve). These action

potentials distort the appearance of the cochlear potential in an unpredictable fashion. At frequencies of 1000 cycles and above, the action potentials produce negligible effects.

The evidence indicates that, after taking account of the sensitivity of the ear at all frequencies, the magnitude of the harmonics in the cochlear response of cats and guinea pigs bears a constant relation to the magnitude of the fundamental, as defined by its maximum value. Thus the second harmonic of a 650-cycle tone appears larger, relative to the fundamental, than that of a 5000-cycle tone, but, of course, the ear is more sensitive to the second harmonic of 650 cycles than it is to that of 5000 cycles. After

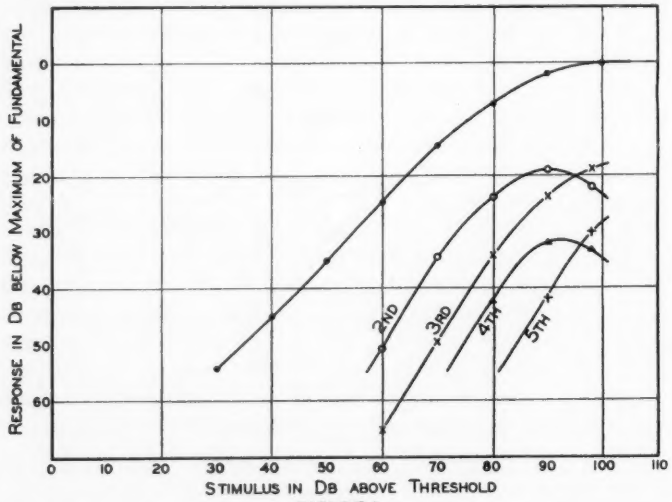


FIGURE 2

Curves for the guinea pig—similar in all respects to those for the cat in figure 1.

making the proper adjustments, we find that, to a first approximation, the aural harmonics, at all frequencies, depend in identical fashion upon the form of the curve relating the size of the fundamental to the intensity of the stimulus. (Measurements were actually made at frequencies of 150, 200, 370, 650, 1000, 1750, 2500 and 5000 cycles.)

It is clear from figures 1 and 2 that the behavior of the even harmonics differs from that of the odd. The odd harmonics appear to arise when the amplitude of motion approaches the elastic limits of the auditory mechanism. The presence of even harmonics must mean that this limit is reached more quickly in one direction than in the other. These considerations suggest that altered tensions on the transmission apparatus of the middle ear could affect the magnitude of the even, but not of the odd, harmonics.

The guinea pig, under a proper dose of dial, shows a convenient disposition to contract its tensor tympani spasmodically. The presence of these contractions indicates a certain functional tonus in the muscles of the middle ear. Deeper anesthesia abolishes these contractions, and decreases the tonus correspondingly (Stevens, Davis and Lurie[4]). By measuring the harmonic content of the cochlear response before and after abolishing the muscle tonus, its effect can be readily measured. Figure 3 shows that alteration of the tension in the tensor tympani produced a marked decrease in the amount of second harmonic, but left the third harmonic unchanged. Similarly, the fourth decreased and the fifth remained unaltered. Hence it appears that the even harmonics are amenable to experimental control through factors which alter the symmetry of the auditory mechanism.

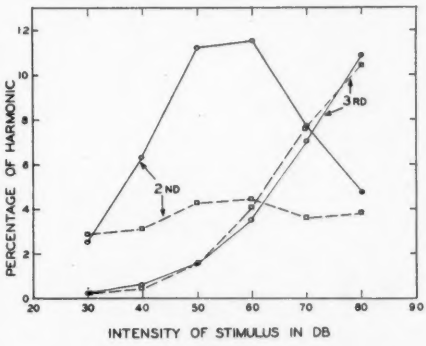


FIGURE 3

Effect of changed tonus of the muscles of the middle ear upon the magnitude of the second and third harmonics. Each curve is an average of values for 1000, 1750 and 2500 cycles. The ordinate scale gives the harmonic content of the response as a percentage of the fundamental. The abscissa represents the intensity of the stimulus referred for each frequency to the intensity necessary for 0.1% of the maximum response of the fundamental. The two bell-shaped curves are for the second harmonic; the sigmoid curves are for the third harmonic. The difference between the dashed bell-shaped curve and the solid curve indicates the change in the second harmonic following relaxation of the muscles of the middle ear. The dashed sigmoid curve shows the almost imperceptible alteration of the third harmonic following this same change. The data is for the guinea pig represented in figure 2.

Finally, we can construct an approximation to the over-all characteristic curve of the ear. To do so, we plot the curve for the response of the fundamental (Fig. 1) in linear instead of logarithmic coördinates. It should be noted that the long linear portion of the former curve is now properly represented as a small segment very near the operating point. The resulting curve represents the upper half of the characteristic curve, as shown in figure 4. The lower half is simply an image of the upper half. Now, if the ear were symmetrical, the position at rest (the operating point) would be at 0. Tension in the muscles of the middle ear, plus other secondary factors, tend to displace the operating point to position A. Then, any sinusoidal force operating about point A will produce a motion having odd and even harmonic components.

From this picture it is clear why the even harmonics in figures 1 and 2 pass through a maximum. When the system is forced to its elastic limit,

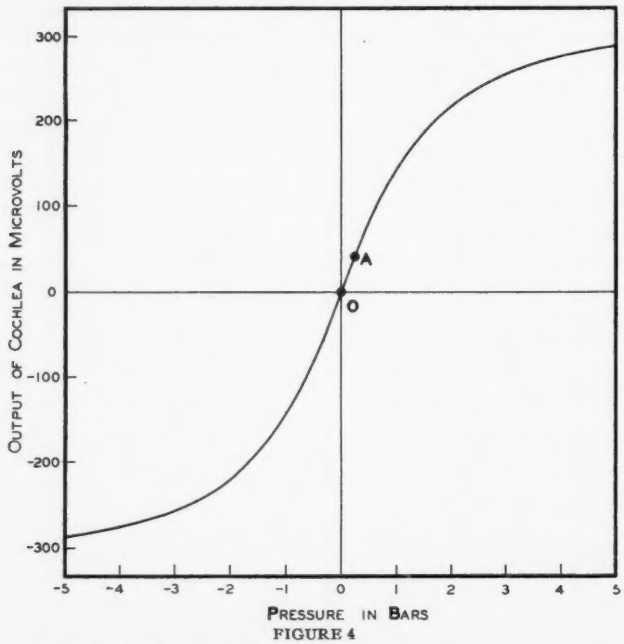


FIGURE 4

Approximate characteristic curve of the ear. The curve relates the electrical output of the cochlea (ordinate) to the applied sound pressure (abscissa). Thus, when the pressure varies sinusoidally about the zero value, the instantaneous voltage in the cochlea can be read from the curve and the resulting wave form determined. When tension in the muscles of the middle ear upsets the symmetry of the curve, it is equivalent to shifting the operating point (point corresponding to zero pressure and zero voltage) from O to A. With the operating point at A both odd and even harmonics are present in the output wave.

so that the cut-off at the two ends becomes more similar, the "wave form" of the resulting motion becomes more symmetrical, which in turn signifies a relative decrease in the even harmonics.

[1] These experiments made use of the combined facilities of the Psychological Laboratory, Harvard University, and the Department of Physiology, Harvard Medical School.

[2] H. Fletcher, "A Space-time Pattern Theory of Hearing," *Jour. Acoust. Soc. Amer.*, **1**, 311–343 (1930).

[3] S. S. Stevens and H. Davis, "Psychophysiological Acoustics: Pitch and Loudness," *Jour. Acoust. Soc. Amer.*, **8**, 1–13 (1936).

[4] S. S. Stevens, H. Davis and M. H. Lurie, "The Localization of Pitch Perception on the Basilar Membrane," *Jour. Gen. Psychol.*, **13**, 297–315 (1935).